Volume LXXV Number 4

THE BOTANICAL GAZETTE

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JUNE 1923

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EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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EDITOR
JOHN MERLE COULTER

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ERRATA

VOL. LXXIV

P. 378, line 7 from bottom, for galbrata read glabrata

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P. 5, line 11 from bottom, for Chamberlain read Chamberland

P. 6, line 19, for phenol-disuphonic read phenol-disulphonic

P. 83, last line, for 1896 read 1869

P. 89, line 4 from bottom, after curves insert (plotted from tables II and IV)

P. 94, line 17, for tissues in read tissues is

P. 119, line 8, for nor read not

P. 126, legend, omit root

P. 155, line 16, for amount read mount

P. 264, line 4 of footnote, for $Ca(NO_3)_3$ read $Ca(NO_3)_2$

P. 273, table III, transpose Uppers and Lowers

P. 289, last line, for as read is

P. 292, line 19, for by comparison read and by comparison

VOLUME LXXV NUMBER 4

THE
BOTANICAL GAZETTE

June 1923

STUDIES IN PARASITISM

A CONTRIBUTION TO THE PHYSIOLOGY OF THE LORANTHACEAE OF NEW SOUTH WALES

JOHN MCLUCKIE

(WITH PLATES XIV–XVI AND SIX FIGURES)

Introduction

The Loranthaceae comprise a remarkably interesting series of plants, some of which are terrestrial autotropic forms, while others are parasitical epiphytic shrubs. The outstanding physiological feature about them is their parasitism. Reduction is always attendant upon parasitism or saprophytism, whether in fungal or angiospermic life; and it seems a reasonable conclusion that parasitism has left its impression on the Loranthaceae, not only in the modified and reduced absorbing system of the mature body, but also in the gametophytic and sporangial structures. The representatives which have been studied most fully are *Arceuthobium oxycedri* (1), *A. occidentale* (4) growing on *Pinus radiata* in California, *Loranthus europaeus*, and *Viscum album* (2).

The Loranthaceae are so well represented in New South Wales by many species which are not found in other parts of the world, that I considered it worth while to study them, and to add my observations upon their physiology to the data already accumulating for the order. There are twelve species of *Loranthus*, namely, *L. celastroides* Sieb., *L. myrtifolius* Cunn., *L. longiflorus* Desr., *L. dictyophlebus* F.v.M., *L. alyxifolius* F.v.M., *L. linearifolius*

Hook., *L. exocarpi* Behr., *L. linophyllus* Fenzl., *L. mayteni folius* A. Gray., *L. pendulus* Sieb., *L. Quandang* Lindl., and *L. grandibracteus* F.v.M. There is also one species of *Notothixos* (*N. incanus* Oliv.), which has a fairly common variety, *N. subaureus* Oliv. *Viscum* is represented locally by two species, *V. articulatum* and *V. angulatum*. All these species are parasitical shrubs, generally with dichotomous branches and opposite leaves. In all the species of *Loranthus* the leaves are thick, fleshy, glabrous, and highly cuticularized. The young shoots of *Notothixos* are minutely tomentose, hoary all over. The species of *Viscum* are quite leafless. In all these forms the fruit is a one-seeded "berry," often developing considerable succulence and color.

Within the order as represented by New South Wales forms, there is every gradation, from large leaves to leafless types. I propose in the course of a few papers to develop a complete investigation, so far as possible, of the physiology of the parasitism of these three genera, *Loranthus*, *Viscum*, and *Notothixos;* and to endeavor to throw as much light as possible upon the origin, development, and degrees of parasitism generally, and the influence this dependent mode of life exerts upon the growth and irritability of the plants studied.

Since *Loranthus* and *Notothixos* are represented by leafy forms, while *Viscum* has leafless species, one might, a priori, anticipate semiparasitism in the former, and a greater degree of dependence of the latter upon its hosts, unless the stem, as in the case of *Cassytha*, assumes the photosynthetic function. At any rate, a leafless parasite would be more likely to show a greater degree of parasitism than a leafy variety. Subsequent work will reveal how far this statement is true.

The material used during this investigation was living, all sections being made from the living material and verified where necessary from preserved material hardened in alcohol. Many observations were made upon the plants growing in their natural habitat, but in every case these were verified by observations upon experimental seedlings raised from the seed under as natural conditions of development as possible. The species at present studied most fully, and which is described in this paper, is *Loranthus*

celastroides. The others will be treated in subsequent studies. I have been very successful in raising young plants of this species upon various hosts in the small botanical garden attached to the School of Botany in the University of Sydney, and in the laboratory; but I was also fortunate in obtaining material of several species in all stages of development from their natural hosts in the bush.

Climatic conditions affecting distribution

Some species of *Loranthus* are confined mainly to the strip of the colony between the coast and the table-lands, where they occur in moist, closely wooded gullies. Others have only been found, so far, in the interior, which is relatively drier than the eastern portion of the state. A few others occur all over the colony. The distribution of *Notothixos* is limited to the zone between the coast and the mountains, while *Viscum* occurs mainly in the northern coastal district. The majority of the species flower between September and December, a few during late autumn. During the spring and early summer the climatic conditions are generally very favorable, especially along the eastern portion of the state, for flowering and fruiting.

The species of *Loranthus*, however, are more numerous in densely wooded areas over the state, particularly in the wooded slopes of the valleys of the Blue Mountains, or along the slopes of the hills skirting the coast line. The prairie type of formation, extending from the coast to the Blue Mountains, with little copses of gums, Casuarinas, and wattles scattered over its surface or along the creeks, is a favorable habitat for *Loranthus*. It appears to flourish equally well along the coast or on the mountains fully 3000 feet higher. This fact may be explained by a consideration of the humidity prevailing in these localities throughout the flowering period. The atmosphere of coastal districts at the time the parasite is flowering and producing its fruits, that is, in summer from November to March, even on very hot days, is extremely humid, the humidity varying from 60 to close upon 90 per cent. The rainfall is erratic but extremely heavy at times. On the Blue Mountains the rainfall is much less than along the coastal districts, as the rain-bearing winds from the south are usually coastal in their distribution,

but in spite of this diminished rainfall, about the time of dissemination and germination on the mountains the necessary amount of humidity is present in the form of mountain mist.

These mists occur throughout the summer period. At any rate, when the seeds are germinating I have seen the entire valleys, with the exception of the edge of the table-lands forming their precipitous walls, enveloped in mist, and it would seem that this mantle of vapor provides in the evening and early morning the necessary moisture condition required for germination. That this is the case is borne out in a remarkably demonstrative manner by the distribution of the *Loranthus* in these valleys. Along the valley bottom and well up its slopes the Eucalypts and Angophoras particularly have innumerable festoons of the parasite; higher up on the slopes it becomes less evident, until on the table-land above it is practically absent.

The actual attachment of a seed to a branch is independent of the moisture conditions, since when the sticky, glutinous gum of the seed coat begins to dry slightly, the seed adheres more firmly to the bark. The prevalence of humid conditions, however, is essential for dissemination, germination of the seed, growth of the root, and probably also for the satisfactory penetration of the bark of the host.

Climatic conditions affecting dissemination

The fruits ripen from about the middle of August to September, about a year after flowering, and not simultaneously. This fact is of some biological importance, as successive ripening of the fruits entails less drain physiologically upon the parasite as a whole. At this time it is interesting to find considerable quantities of reserve starch in roots and stems, showing that the parasite's foliage is capable of considerable synthesis. Moreover, this period is generally characterized by considerable rainfall over the coastal districts, and by mists in the valleys of the mountains. The humidity, therefore, is generally comparatively high when many fruits are ripening and dissemination is active, varying from 60 to over 80 per cent.

Heavy rainfall, with or without wind, generally causes great loss among the seeds of *Loranthus celastroides* and other species, for the adhesiveness of the gelatinous coat is diminished when the

surface of the object is wet, and particularly ineffective when subsequent raindrops tend to loosen any slight adhesion which may be made. The most favorable conditions for dissemination are a light shower of rain followed by warm sunshine. Under such circumstances the fruits swell and become turgescent, the gelatinous base of the seed swells, the absciss layer at the base severs the stalk and seed, and the "operculum" is lifted. These changes take place quite rapidly after rain has fallen during the last phases of ripening of the fruits.

A high humidity acts in the same way, especially where the *Loranthus* forms numerous dense thickets or clumps upon the host. In such positions any moisture present in the air of these thickets, or upon the parasite or host itself, will be retained and have a somewhat stimulating and favorable effect upon dissemination, inasmuch as there will be a relative psychometric difference between the air of the clumps of the parasite and the surrounding air, sufficient to effect dispersal of the ripe seeds. At any rate, the moisture in the air of such clumps of the parasite will tend to reduce transpiration from the leaves and fruits, and will thereby serve to materially and rapidly increase the turgid character of the fruits. Furthermore, less transpiratory activity from the leaves of the host in and about the thickets will make more water available to the haustorial tracheae of the parasite, and in turn to the fruits. As far as I have been able to determine experimentally, the fruit coat does not absorb moisture, and the rapidly increased turgidity of the ripened fruit, culminating in dissemination, is dependent upon reduced transpiration in an atmosphere where the humidity is increasing. Under such conditions of reduced transpiration, especially after rain has provided the host tissues with more water, the fruits become large, soft, and succulent, considerable pressure developing within, and the abscission layer at the base of the fruit will be a line of mechanical weakness, as also will the circular line of dehiscence around the apex of the fruit. Since the fruit is pear-shaped, broad at the apex, narrow at the base, it will fall apex first, so that the force of impact will precipitate the rupture of the apical line of mechanical weakness; the extrusion of the seed then follows. After careful studies of large numbers of living fruits of *L. celastroides*,

I am convinced that the factor in developing internal pressure is the swelling of the walls of the gelatinous zone at the base of the fruit. If dry sections of the fruit be mounted on a slide and then irrigated with water, the swelling of the gelatinous walls is seen very distinctly. The lumina of the cells become practically obliterated. Under such circumstances, it is not likely that the contents of the cells increase their osmotic properties, and that the expulsion of the seed is due to their increased osmotic pressure, rather than to the mere simple swelling of the gelatinous cell walls by imbibition of water.

Fruit

It is now well known from the investigations of PEIRCE and JOHNSON that the fruits of *Arceuthobium* are explosive, that dissemination takes place by the forcible ejection of the seeds from the fruit, and that the anatomy and mechanics of the fruit are of such a nature that considerable explosive force may be developed, leading, when the necessary climatic conditions are presented at maturation, to forcible expulsion of the glutinous or gelatinous coated seeds. Although the anatomy of the fruit of the species of *Loranthus* which I have so far studied somewhat resembles that of *Arceuthobium*, there is no evidence from dissemination under the natural conditions of the native habitat, or the approximately natural conditions of experiment, that there is explosive ejection of the seeds. Dissemination involves rather a gradual extrusion of the seed in *L. celastroides* (figs. 1–3). This will probably be better understood after a description of the anatomy and mechanics of the fruit. The fruit is a false type, being composed of the succulent receptacle which is adnate to the ovary, as in *Arceuthobium*. The following distinctive zones or layers may be distinguished in a longitudinal section, passing from the periphery inward (fig. 4).

1. The epidermis with a few stomata and thick cuticle.

2. A narrow zone of small cells with thick cellulose walls and little protoplasm.

3. A broad zone of large cells with collenchymatous thickenings, abundant protoplasm, and pitted walls, elongated parallel to the surface of the fruit. This terminates in a layer of narrow cells with thin walls, to which is attached the next zone.

4. In the lower half of the fruit a broad zone of cells with mucilaginous walls, little protoplasm, and no chlorophyll. These cells appear to be compressed in young fruits, as they assume a crinkled, wavy form, as if development and elongation were inhibited. They are long and narrow, and elongated parallel to the long axis of the fruit. This zone tapers off toward the middle of the fruit at about the level of the base of the embryo sac. A sheath of this envelops the seed.

5. Within this mucilaginous zone is situated another distinctive broad tissue containing some chlorophyll corpuscles and starch grains. This appears green even in the ungerminated seed, and surrounds the endosperm within. It is narrower at the base, where the former zone is so well developed, and broader in the upper portion of the fruit. The cells have thick mucilaginous walls, and radiate outward from the endosperm zone.

6. The endosperm containing abundant starch grains, and composed of small cells with intercellular spaces.

7. At the apex of the endosperm is the small green embryo. Even before germination the embryo contains chlorophyll.

8. From the base of the endosperm to the base of the fruit there is a central shaft of tissue which forms a stalk supporting the endosperm.

Structure of seed

In most essential respects the seed of *Loranthus celastroides* resembles that of *Arceuthobium;* morphologically it is more than a seed, part of the ovary being present. It has a thick gelatinous coat, which dries readily on exposure to air and causes the adhesion of the seed to any object (figs. 5–7). On account of its gelatinous coat the seed is able to obtain water from the air, as rain, dew, or vapor. The gelatinous coat swells and fits into any unevenness of surface, thus securing firmer attachment of the seed. All the water required during the early growth of the embryo is absorbed by the gelatinous covering. The seeds when found upon the tree have a shriveled brownish coat (the remains of the fleshy covering left by the birds) which is highly glutinous, and this gummy substance very effectively causes the seeds to adhere to the bark. The bark upon which they are generally found is comparatively smooth, with the exception of

Banksia, which is exceedingly thick, rough, and corky. Seeds are often found upon the younger branches which have not nearly such thick bark, and penetration is therefore more easily accomplished.

This gelatinous covering is capable of absorbing water and retaining it, and therefore, as PEIRCE (4) has suggested for *Arceuthobium*, it is the only means by which the young embryo can obtain water until it has penetrated into the water-conducting tissues of the host. This gelatinous coat retains water most tenaciously. It is highly significant that the glutinous, gelatinous covering is not only adapted for securing the adhesion of the seed to the twigs, but that it also proves such an effective means of absorbing water in the form of rain, dew, or vapor, because germination of the seed demands a general moist atmosphere and environment.

Dissemination in L. celastroides

NATURAL

The fruits of this species are large, pear-shaped, and yellowish green. When ripe they are soft and pulpy, greenish at the base and yellow at the broad end. At this upper end a distinct, circular line of dehiscence is developed, which provides for the rupture of the fruit and the subsequent liberation of the single highly viscid seed (figs. 1–4). The slightest pressure upon the narrow base of the fruit causes splitting of the coat along a part of this line of dehiscence, so that the broad end of the fruit lifts up as an operculum as the seed passes out. There is nothing of an explosive character about the dissemination. In some species of *Loranthus* this very essential aspect of propagation appears to be dependent upon the agency of birds, or upon the automatic rupture of the fruits themselves by the swelling of the inclosed seed, and in some species upon both factors.

In plants of *L. celastroides* which had almost completely enveloped large trees of *Eucalyptus corymbosa* in French's Forest, New South Wales, I found hundreds of fruits lying on the ground beneath the trees. Many of these were not nearly ripe, and were quite hard and non-succulent, wind very probably having shaken them off. Others, however, were perfectly ripe and soft, and apparently had fallen off in natural course, as on striking the

ground the operculum had been raised, probably by the force of impact, and the seed had partially escaped. Undoubtedly strong wind at the time of ripening has a disastrous effect upon dissemination, as many hundreds of fruits are shaken off directly to the ground. This is facilitated by the provision of the absciss layer at the base of the fruit, where it is attached to the stalk (fig. 4). I have observed in this relation that on shaking the plants numerous ripe fruits fall. Since in this species many of the branches are pendulous, and hang down far below any branches of the host, it is inevitable that a great percentage of the fruits are lost. This wastage in *Loranthus* is remarkably severe.

On the other hand, when the fruits are produced on the upper branches of the parasite, so that masses of foliage and branches of the parasite and host are directly below the fruits when falling, many of the seeds actually succeed in securing attachment to some object. In experiments in the field, I have observed that ripe fruits dropped from the upper branches of the parasite almost invariably strike a branch or a leaf, and rupture. The sudden impact, combined with the slippery, turgid nature of the seed, causes the latter to glide out of the fruit (figs. 1–3). It rarely happens that the seed remains attached to the first object met with, but mostly to the second obstacle. This, however, depends upon the height of the fruit above the first object in its path. When this distance is short, the downward velocity of the fruit is not great, and the gelatinous covering of the seed is able to arrest and stop its movement.

It is a noticeable feature that the viscidity of the gelatinous coat increases on exposure to air. The whole seed has a yellowish white appearance, excepting the basal gelatinous structure which is whitish in color, and endowed at the moment of dissemination with a decided elasticity. In seeds just freed from the fruit the cells of this gelatinous base are arranged in long, crinkled, more or less coiled filaments (fig. 4), no doubt owing to the prevention of their elongation when inclosed in the fruit, so that when the seed escapes from the fruit, these filaments of cells straighten out and their length increases enormously. This elongation has an interesting bearing upon the adhesion of the seeds to supports, for obviously the

slow straightening out of these masses of gelatinous filaments will have the effect of slowly arresting the fall of the seed. This stretching of previously folded filaments or masses of cells seems to explain the occurrence, in the bush, of seeds hanging by long masses of a whitish gelatinous substance, sometimes 0.5–1.5 inches in length, to branches or the edges of leaves. Where the seeds are liberated upon a pendulous leaf, a gummiferous-like streak is apparent where the seed glided over the surface for some distance. Many seeds were found germinating upon the lower surface of twigs, upon the trunks of trees, and upon fences beneath the parasite, just in the position where they dropped.

The time of dissemination shows an interesting relation to the degree of humidity in the atmosphere and the consequent rate of transpiration. During very dry days humidity is low, the air surrounding the plant is dry, and transpiration, therefore, is fairly active from host and parasite alike. The amount of water available to the ripened fruits, inducing swelling of the tissues involved in dissemination, is therefore limited and insufficient. During such periods or conditions none or few seeds are liberated from the fruits, unless the latter be shaken off by wind and rupture on striking a branch or the ground. On the other hand, during dull, warm, moist days humidity is high, sometimes attaining 95 per cent, transpiration is considerably reduced, and therefore the amount of water in the tissues of the host and parasite is greater. Much of this water reaches the ripened fruits of the parasite, causing the motor tissues concerned in the rupture of the operculum of the fruit and the forcible extrusion of the mucilaginous seed to swell and perform their work. The difference in the water content of ripened fruits during hot and dry, and dull and moist days makes itself apparent in longitudinal sections cut immediately from fruits plucked from the parasite and examined without delay, and also in their general degree of turgidity under these different conditions.

BIRDS

Although the structure of the fruit of *L. celastroides* is of such a character that the seeds will ultimately be ejected, if the necessary climatological conditions are present, there is a certain degree of

succulence and color at maturity which makes them attractive objects to birds. The fruits of *L. linearifolius* are succulent and white, those of *L. exocarpi* orange red or blackish purple, those of *L. linophyllus* red, globular, and very succulent. Succulence and color are generally most pronounced in the forms growing in the drier interior. The remaining species have usually a fairly succulent, soft, pulpy, and greenish yellow fruit. All the species are sufficiently attractive to secure dissemination by the agency of birds. The normal, natural, and passive mode of dissemination, previously described in detail, accounts for the occurrence of young plants of the parasite beneath centers of previous infection, but the only possible explanation of the occurrence of isolated forms of the parasite high up on surrounding trees is their being carried there by birds. This will be discussed more fully in the very succulent species *L. linophyllus*, in a subsequent paper.

Wind

By means of wind seeds may be deposited upon branches somewhat remote from the branches they would fall upon by the action of gravity.

Structure of seed

The seed is covered externally by a thick gelatinous coat, composed of oblong-shaped cells arranged almost perpendicularly to and radiating out from the surface of the seed. These cells have a distinctive firm middle lamella of cellulose material, and are thickened by a broad zone of mucilaginous material, which swells considerably on the application of water. The whole layer may swell to several times its original size on absorbing water. The walls form the conspicuous feature of these cells, the cell cavity being relatively narrow. The mucilaginous zone is attached to a brownish, slightly sclerotic layer, which is followed inward by the cells of the endosperm. Both on the inner and outer surface the endosperm cells are small. Toward the center the cells are larger. Abundant starch is present in the form of small roundish grains in these cells.

The mucilaginous zone on the exterior of the seed of *L. celastroides* is of the highest significance in the germination and early development of the parasite. It is the means of supplying the water

required for germination, for the mobilization of the food reserves in the endosperm, and it is the means whereby the seed is securely attached to some object. It has been explained previously that the gelatinous zone is strongly developed at the base of the seed, and the individual cells are longitudinally elongated but strongly crinkled. These cells are stretched when the seed impinges upon an object, and finally contract, owing to drying by the air. The contraction finally brings the seed close to the branch. The absorption of water by the gelatinous seed coat causes a swelling of individual cell walls, and the approximation of a larger surface of the seed to the branch. PEIRCE (4) has observed similar mucilaginous cells in *Arceuthobium*, but, so far as my observations show, the middle layer of the cell wall is not spirally thickened. Once a seed has become firmly attached to a branch or a leaf it can only be removed with difficulty. The gelatinous covering appears to gain in adhesiveness on exposure. Heavy rain sometimes washes away many seeds which have become partially attached, by increasing the slippery property of the seed coat, and thereby diminishing its adhesiveness. It is common to find large numbers of seeds of last season, which have failed to germinate, still attached to the host or to the posts of fences or gates wherever the seeds happened to be deposited by natural or artificial dissemination.

As one might expect, the seeds of *L. celastroides* germinate upon anything, living or dead. I have observed germinating seeds on fences, gates, on the soil, dead leaves or twigs on the ground, trunks of trees, branches, or on leaves. Large numbers of seeds for some reason or other fail to germinate. During germination a humid cloudy atmosphere with occasional rain is necessary. The seed coat is then able to obtain the necessary water. If dry weather follows immediately upon dissemination, the seeds may not germinate at all, but remain dormant for a few weeks, germinating then if conditions are favorable. When favorable conditions are presented immediately after dissemination, germination takes place in three or four days. *L. linophyllus* is most rapid in this respect, *L. celastroides* requiring about seven or eight days. This rapidity of germination is interesting in such parasitic forms, as a shortening of the period required for germination means that the seedlings

attain maturity rapidly during the period when favorable conditions for growth are generally present.

Before germination, the embryo appears as a small, cylindrical body extending from the micropylar end of the seed to two-thirds the length of the embryo sac; it is surrounded closely by the endosperm (fig. 4). There is no evidence of plumule or distinctness of cotyledons until germination begins, when a groove appears between them (fig. 10). The whole of the embryo contains chlorophyll while retained within the seed, excepting the dermal layers of the cotyledons, which are clear and in contrast with the remainder of the body. The cotyledons remain imbedded in the endosperm, growing as the embryo grows, and encroaching upon the endosperm tissue. They function as haustorial organs. There is no evidence of starch in the embryo while in the seed immediately after dissemination; this appears later during germination.

Germination

When freed from the fruit covering, the seeds of *L. celastroides* adhere to whatever object they have struck when falling, or upon which they were discarded by birds. The gelatinous coat of the seed is soft, slippery, yet viscid. The seeds often glide from the upper surface of a branch to the lower, and hang down by longer or shorter attachments, formed by the elongation of the gelatinous cells at the base of the seed. In such circumstances streaks of gelatinous or sticky matter are left on the surface of the branches or leaves. The sticky base of the fruit, however, fits closely to any unevenness of surface, and soon arrests the gliding movement of the seed over the object it has touched. It is a matter of chance whether seeds become attached to living parts of plants or to dead twigs or leaves, but this fact does not in any way interfere with their germination. In the natural habitat of the plant I have found the seeds germinating on living twigs and leaves, on the bases of older stems, on dead twigs, branches, leaves either attached to a living plant or on the ground beneath the clumps of the parasite upon the host. I have observed also that the seeds will germinate readily in the laboratory or in a frame, attached to living plants or to pieces of wood. I have succeeded also in germinating seeds on

a slide kept in a moist illuminated chamber and on moist sand in a Petri dish.

For germination, certain factors are absolutely essential, namely, an adequate supply of food to the embryo imbedded in the nutritive endosperm, moisture, favorable temperature, and light. The moisture is required to maintain the turgidity of the embryo tissues during germination, and to act as a vehicle for the translocation of the foods stored in the endosperm, and required by the embryo. While the seed has not established organic connection with the xylem of the host, the only available source of moisture, of course, is the atmosphere, and in the matter of supplying the embryo's requirements as regards water, the gelatinous viscid coat is significant. This coat readily absorbs moisture in the form of vapor, rain drops, or dew, and by placing drops of water upon the seed coat, it is readily demonstrated that the gelatinous covering swells. In sections of this coat mounted dry and then brought into contact with water, it is seen that the cell walls, by virtue of their highly gelatinous character, swell considerably and become almost transparent and difficult to see, with the exception of a central middle lamella, which appears to have a firmer consistency, texture, and a different constitution from the remainder (figs. 8, 9). This gelatinous coat of the seed, therefore, as appears to be the case in *Arceuthobium oxycedri* (1) and *A. occidentale* (4) also, acts as a water absorbing region, and a water reservoir for the embryo. While it loses water with difficulty to the atmosphere, it appears to part with it readily to the embryo, as indicated by the rapid changes occurring in the seed after the supply of water has reawakened its activity.

The root of *L. celastroides* is invariably short, generally attaining a length of 4–6 mm., and seldom exceeding this, unless when growing over a smooth surface of a leaf or twig. Among the leaves and twigs of the hosts, sufficient obstacles to growth of the root are frequently presented. It is a common occurrence to find germinating seeds held fast between two leaves or twigs, and the root growing downward toward the stem, and being obstructed in its growth after attaining a length of a few millimeters. As will subsequently be shown, the root of *Loranthus* appears to be more sensitive to stimuli, especially light, than that of *Arceuthobium*, and

therefore in response to this stimulation meets with obstacles to its growth more frequently. In addition to satisfactory moisture conditions, light exerts an important influence upon germination. In the embryo, even inclosed within the fruit, some chlorophyll is present, especially in the cotyledons and hypocotyledonary region. If the seeds are kept in a moist atmosphere in the dark, no further development of chlorophyll takes place, but if the seeds are illuminated, germination ensues in four to ten days, and the amount of chlorophyll increases in the whole of the embryo, even in the root (figs. 11–16). Experiment indicates that light is just as essential for germination as moisture, as seeds will not germinate in the dark, even though conditions as regards moisture and temperature are favorable.

The first organ of the body to appear is the root. This is a small conical growth devoid of a root cap. The apex, as it grows through the enveloping gelatinous matrix, retains a covering of this, which probably functions as an efficient root cap, absorbing water and preventing the drying of the root apex. The root may grow out in any direction from the seed, but immediately turns toward the branch to which the seed is attached. In all the specimens studied in *L. celastroides* on *Banksia*, *Casuarina*, *Eucalyptus*, or *Angophora*, the root has been comparatively short, seldom exceeding half an inch in length. On coming into contact with the branch, it develops a large, swollen, club-shaped end, which owing to the force of the growing part behind is pressed into close contact with the bark. This terminal disc is the holdfast (figs. 17–22). This close relation between the root apex and the bark of the host is the essential preliminary to penetration by the root. The haustorium which develops into the host tissues is really a portion of the root tip (fig. 18).

The root is short, and shows varying amounts of curvature, depending upon the position of the micropylar end of the seed in relation to the branch. Where the latter is in close proximity to the branch, the root may not exceed 0.25 inch in length. All the young embryos studied have a very short root, which in no case grows indefinitely along the branch to which the seed was attached. The irritability of the root to gravity, contact, and light will be discussed later.

The holdfast is an essential preliminary to the development of the haustorium, and is the enlarged disclike end of the primary root. Its development depends upon contact with some obstacle to the growth of the root, when the holdfast is formed immediately. Experiment shows that without such resistance the root remains slightly club-shaped or conical. Seeds of the parasite were germinated in a moist chamber upon pins passed through the antipodal end of the seed and attached to corks. The roots appeared in due course, and retained their conical or slightly club-shaped form until the seedlings died, owing to the exhaustion of the foods in the endosperms. On the other hand, roots which were brought into contact with some object that resisted growth in every case developed the holdfast. The holdfast invariably precedes the formation of the haustorium, and is simply a structure analogous to the cushion of *Cassytha* or *Cuscuta* (**2, 3**) for securing a firm attachment of the parasite to the host, preparatory to the development of the haustorium. Experiment clearly demonstrates that the development of the haustorium depends upon contact. It appears in the case of *Loranthus* immaterial whether glass rods coated with wet or dry gelatine, or without this covering, or other rods be used; contact with them stimulates the formation of the holdfast, and finally of the haustorium. If the root remains in contact with the obstacle for twenty-four hours and then is removed, the holdfast will develop into the typical disc form. It normally assumes a flattened form, its margins being slightly raised, its center slightly depressed, so that the peripheral zone comes into close contact with the object, living or dead. Where a thin experimental rod is used, the margin of the holdfast may partially clasp it.

While the root is growing, and before the formation of the holdfast, many of the epidermal cells in the conical apex develop into short stiff hairs, which have thin walls, are densely protoplasmic, and secrete a reddish glistening fluid (figs. 23–25). These hairs have two properties, sensitivity to contact, and the securing of a firmer attachment to any obstacle. They may also, together with the glutinous covering of the root tip, serve to retain water or even to absorb it. At any rate, if they are removed from the root the holdfast does not develop as soon as when the hairs are present.

Furthermore, they occur in largest numbers at the knoblike end of the root; that is, the portion nearest the host branch or rod used in the experiment. Their development in this zone of the root also serves to attach the disc more firmly to the bark of a branch, into the crevices of which they grow. They render the attachment between host and parasite more secure than it would otherwise be if it depended upon a smooth surface of the root. The attachment of the disc is strengthened by modifications which take place in the outer walls of the epidermal cells of the disc, especially those centrally placed. Their walls become thicker, owing to the formation, probably from the original material of the wall, of a brownish red gelatinous substance which cements the epidermis of the disc to the bark of the branch of the host.

While this development of the root is taking place, the hypocotyl elongates and appears outside the seed. It is usually split longitudinally, and from the base of the split, near the root, the small narrow green leaves are developed (fig. 16). The cotyledons remain within the seed, providing the developing embryo with nourishment.

Before the appearance of the haustorium which develops from the central part of the holdfast, or from that part most intimately applied to the host branch or rod, the root consists of a mass of actively meristematic cells nearest the apex, limited by a peripheral layer or dermatogen, the cells of which may assume the highly papillate form of the cushion of *Cuscuta* (**2**) or *Cassytha*. Farther from the apex the central axis of the root is composed of tracheae. If contact with the host branch is maintained, the central zone of the disc grows out into the conical haustorium, which ultimately penetrates the opposing tissues. The factors involved in the penetration of the haustorium into the host will be discussed later.

Nourishment of embryo

A longitudinal section of the seed after germination shows the embryo situated at the upper end of the endosperm, surrounded on all sides by this nutritive tissue. The cotyledons are toward the center of the endosperm, and their tips are in close contact with the endosperm cells. There is no visible space between them and the

endosperm, no intervening zone which could be filled with fluid and across which soluble foods might be transported to the embryo (fig. 10). Farther from the apex, however, there is a distinct space between the cotyledons and the endosperm cells. The endosperm nearest the embryo is delimited by a layer of small cells. Beyond this layer the cells enlarge; the former are characteristically almost free from starch grains, the latter full. Air spaces appear between the cells. The amount of starch increases from the embryo outward.

The embryo itself is limited by a layer of small cells representing the dermatogen. These cells are colorless, and, in contrast with the other cells of the embryo, devoid of chlorophyll. They are densely protoplasmic, with a large nucleus, and have the general appearance of a secretory or digestive layer. At the apical zone of the cotyledons, the contact between them and the surrounding endosperm is extremely intimate, their walls abutting each other. With such a close approximation, enzymes secreted by the dermal layer of the cotyledons could diffuse readily into the storage cells of the endosperm. Farther back from this apical zone any enzyme secreted by them must diffuse across the narrow space separating them from the endosperm. All the cells of the endosperm nearest the peripheral layer of the cotyledons contain starch grains in all stages of solution. The cells immediately behind this layer have more numerous grains, some of which also show signs of partial disintegration. Structurally the dermal layer of the cotyledons of the embryo has the appearance of active secretion and digestion, and is probably the actual source of the enzymes which dissolve the starch of the endosperm cells. It is only necessary for the enzymes secreted by the cotyledons to reach and act upon the contents of the nearest layer of endosperm. Solution in the more remote layers would be brought about by enzymes produced in these cells themselves, as a result of the stimulus emanating from the superficial endosperm cells in contact with the cotyledons. There could also be established readily an osmotic flow of dissolved food from the interior of the endosperm to the absorbing cotyledons. The latter are purely haustorial structures, and remain within the

seed coats until every particle of food is removed. Although they contain some chlorophyll, they do not function photosynthetically.

Irritability of primary root

ACTION OF GRAVITY.—The root of the young plant of *L. celastroides* is quite unresponsive to geotropic stimulation, its direction of growth varying with the position of the seed upon the branch, sometimes growing directly upward or downward, as the case may be. Such wide ranges of direction are incompatible with sensitivity to the action of gravity. A mere superficial examination of young seedlings attached to the branches of trees will show that the root grows in any direction at first, and finally turns downward to the branch, generally meeting the surface at right angles. There are, however, a few exceptions to this mode of development. Occasionally seedlings were found attached to the edges of a branch or to the lower surface, in such a position that, if downward growth of the root was a constant feature of development it would inevitably fail to gain contact with the tissues of the branch. In these instances the root showed a curvature in a plane forming practically a right angle with the axis of the branch (figs. 19–22). From observation of the seedlings growing under natural conditions, therefore, I should support the view that in its growth the root is not influenced by gravity acting upon it, and therefore the curvatures it may make are not of a geotropic nature. Seedlings cultivated in a moist chamber in darkness developed their roots in all conceivable directions, the direction apparently being determined not by gravity, but simply by the position of the micropyle. The roots in such circumstances grow straight out into the air.

ACTION OF LIGHT.—On the other hand, experiment demonstrates the presence of decided irritability to light. The roots are negatively phototropic, invariably curving away from the center of illumination. Numerous experiments were performed with the germinating seeds of *L. celastroides*. Some were attached to small plants of *E. globulus*, *Acacia discolor*, etc., in pots in a heliotropic chamber, the funnel admitting direct sunlight being 3 inches in diameter, so that the apex of the radicle was pointing directly

toward the light, the seed being horizontal. The roots invariably curved away from the light, sometimes downward along the lower side of the seed, sometimes upward and backward, at other times back along the flank of the seeds. These results again confirm the absence of any geotropic response (text fig. 1). Another series of seeds were fixed in a vertical position, the root just ready to emerge. In every case the roots grew away from the light, generally obliquely upward and backward (figs. 26, 27). A third series

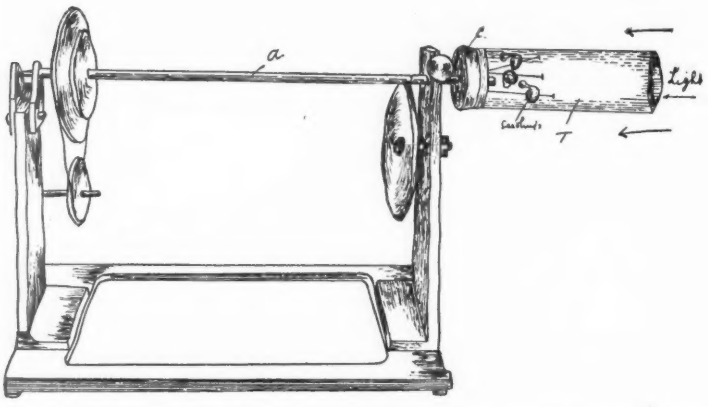

FIG. 1.—Apparatus used to determine whether roots of *Loranthus* are heliotropically sensitive: seeds germinated in moist chamber made from large collecting tube (*t*), attached by means of pins to cork (*c*) of tube; tube then fixed to revolving arm of klinostat (*a*); apparatus then placed in heliotropic cupboard admitting a unilateral beam of light upon seedling; roots of seedlings invariably grew away from the light.

of seeds were fixed horizontally, so that the micropylar end pointed directly backward. In every case the root grew horizontally toward the dark.[1] Experimental work, therefore, distinctly proves that the roots of *L. celastroides* are negatively phototropic, and bears out the evidence from the growth of the roots in their natural habitat.

[1] A series of seeds were attached by pins to a cork fitting into a tube containing moisture, which was fitted to the revolving arm of the klinostat. The apparatus was then placed in an heliotropic chamber, with the light falling upon the seeds from one side, and gravity eliminated (text fig. 1).

It is advantageous to the root of this parasite to be unsensitive to gravitational stimulation, and to possess strong negatively phototropic irritability. In every case, no matter in what position the seeds may germinate upon a host, a negatively phototropic curvature will bring the root into contact with some part of the host. So far as I can determine experimentally, it is the extreme tip of the root which possesses the sensitivity, and the actual mechanism of curvature appears to be located in the portion of the hypocotyl near the root. Roots illuminated from the side grow away from the source of light; if the source of light is above the root, it grows downward. A minute tinfoil cap placed upon the root tip inhibits perception of a direct light stimulus.

The root just at the time the footlike, club-shaped end is developing consists of a mass of parenchymatous cells, with thin walls, nucleus, and protoplasmic contents. The nutritive materials from the seed are also transferred to the root, and are seen in considerable quantities in its parenchymatous cells. The seed becomes shriveled and dried as the foods are removed, and finally may be blown away or remain attached to the branch until washed off by rain.

Haustorium

The haustorium develops from the central zone of the holdfast, and penetrates through the cortical and phloem tissues of the host into direct relation with the xylem (figs. 28–31). The apex of this mass of haustorial tissue is pointed, the base broadens out, thereby encroaching upon the cortex of the host. There is great destruction of tissue, cortex, phloem, and cambium suffering successively in the line of growth of the haustorium. As far as I can determine, the haustorial tissue is not definitely confined to the medullary rays in its inward progress. At first the haustorium consists of a broad, conical mass of parenchymatous cells, which are actively meristematic, with dense cytoplasm, thin walls, and large nuclei. On reaching the cambium, the apex often spreads out along the layer (text fig. 2). The cells of the central core at the base of the

FIG. 2.—Apex of haustorium (*H*) spreading along the cambial zone of stem of *Banksia latifolia;* nat. size.

haustorium are meanwhile differentiating into short, reticulately thickened tracheids characteristic of most of such parasites. Later, when the apex has reached the vessels of the host and applied itself to their walls, the haustorial cells in actual contact differentiate into tracheids, those immediately behind do so also, and so connection is established between the basal series of the haustorium and those apical tracheids in contact with the water tissues of the host. Large quantities of food were observed in young haustoria just penetrating through the cortex of the host. It is difficult to say whether these were derived from the host tissues or from the seed, as in some instances food was present in both. In other cases, however, there was no reserve food visible in the host tissues, yet abundance was present in the haustorium situated in the cortex of the host. The amount of food in the seed is sufficient to nourish the embryo for several weeks. This time is sufficient to permit of a linking up of the host tissues with those of the parasitic haustorium.

Subsequent developments in the haustorium follow rapidly. The base is widened, lateral outgrowths penetrate obliquely through the cortex, and tap other xylem tissues of the host (fig. 32). As in *Viscum* (2), masses of the haustorial cells in the cortex develop into aerial branches which grow outward and upward through the cortex of the host bearing the foliage leaves (figs. 33, 34). One or more secondary roots may also arise from this comparatively undifferentiated haustorial tissue in the host. These grow outward through the host's tissues, and spread over the surface of the branches, sending other haustoria into the host at intervals (figs. 35, 36). From these new leaves and finally flowers are developed. By means of these secondary roots the infection is spread sometimes over the whole tree. This development is very similar to that of *Arceuthobium* and *Viscum*, and affords an example of the generation of a complete plant from a portion of a root.

Morphologically the haustorium is of root origin. It is part of the primary root of the seedling developed as a special haustorial apparatus. All subsequently formed organs are derived from this mass of haustorial tissue in the host. Physiologically the haustorium functions as a root.

Factors involved in penetration of haustorium

It has already been shown that the root of *L. celastroides* is not sensitive to gravity, but is strongly negatively phototropic. The latter property makes it tolerably certain that the root tip will, often after a curvature of 180°, gain contact with a branch or leaf of the host. If the axis of the root form a right angle or approximately a right angle, or if it meet with some obstacle to its forward growth, then the disclike holdfast and the haustorium develop. This contact or this resistance to growth is an essential preliminary stimulus to the formation of the holdfast and the subsequent development of the haustorium. If the contact is made for a time and then broken, the haustorium will develop as a small whitish papilla in the center of the disc.

For the penetration of the host tissues several conditions are necessary, namely, a firm attachment of the seed to the branch, resistance to the forward growth of the root apex producing the holdfast, the development of the growth pressure by the root, and chemical action of the epidermal cells of the haustorium. In sections of young haustoria which are just developing against the peripheral corky tissues of a host branch, it is evident that the outer series of cells just beneath the haustorium are pressed inward. Evidence of pressure may also be seen along the edge of the haustorium where it enters the cortex, the outer layers of cork frequently being pressed inward at these points. Farther in, no pressure effects are visible, so that the progress of the haustorium depends on some other factor. That pressure is an essential preliminary of penetration of the peripheral tissues of the host is confirmed by experiment. A thin strip of smooth wood about 0.25 inch thick was fixed firmly to a clamp. From this wood a small piece was cut out, slightly smaller than the area of the holdfast of the parasite. A thin film of rubber was fixed across the open end of the cut. A seedling firmly fixed to a small *Eucalyptus* plant, whose root had grown out into the air, and by contact with an object had been stimulated to develop the holdfast, was then brought into relation with the rubber film extending across the slit in the wood block (text fig. 3). The whole apparatus was then placed in a moist chamber and kept there for several days. During this time the

haustorium developed as a conspicuous, white, conical papilla and pressed against the rubber over the slit. This was forced inward a short distance in front of the haustorium, showing that a certain degree of pressure is exerted by the developing haustorium, but this force is undoubtedly associated with a more potent one, namely, chemical solution. In this experiment the point of contact of the haustorium and object is marked by a glistening spot, as if an enzyme were secreted by the haustorial cells. If the rubber is coated with a thin film of starch, many of these grains will be partially dissolved in a few days, by the solvent action of this secretion. The absence of crushed cells in the host along the path of the haustorium, and the intimate association of haustorium and host tissues, confirm the view that chemical solution is an important factor in the penetration of the haustorium and its subsequent ramifications within the cortex of the host.

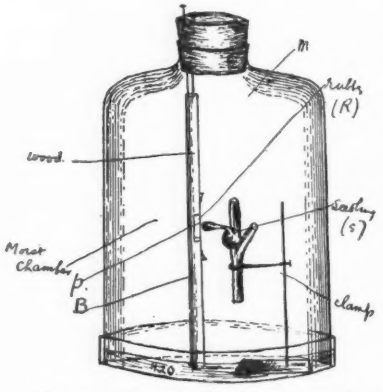

FIG. 3.—Moist chamber (*M*), to cork of which is fixed by means of large pins a smooth branch (*B*), from which a small portion (*b*) has been cut out and opening covered with rubber film (*R*); seedling (*S*) attached to small branch, clamped in such position that apex of root touches rubber film (*R*); growth presses rubber inward.

Structure of host in relation to penetration

L. celastroides occurs most commonly upon *Eucalyptus paniculata*, *E. siderophloia*, *E. eugenioides*, *Acacia mollissima*, *Angophora lanceolata*, *A. intermedia*, *Banksia latifolia*, *B. serrata*, and several species of *Casuarina*. These have all comparatively thick, rough barks, to which the sticky seeds adhere. Unevenness of surface provides numerous obstacles which resist the growth of the root and assist in penetration. This thick bark appears to be penetrated readily by partial solution and pressure.

Seeds were germinated upon the phyllodes of *Cactus* and the thick fleshy leaves of *Agave* and *Aloe*, but the root was unable to

penetrate through the thick cuticle. I have found in nature numerous germinating seeds upon leaves of *Banksia latifolia* and *B. serrata*, and have kept them under favorable conditions of moisture and light for some time in the laboratory, but have not been successful in obtaining cases of the haustorium penetrating through the cuticle. This may be due to the absence of an enzyme from the parasite root, which is able to dissolve the thick cuticle of these leaves. This makes penetration dependent upon pressure alone, but sufficient pressure does not seem possible where the seeds are germinating upon a leaf, on account of the absence of the necessary resistance to growth of the root. The haustorium of *Cassytha* does penetrate the thick cuticularized leaves of *Xanthorrhoea graminifolia*, *B. latifolia*, etc., but the parasite receives the necessary resistance to haustorial growth for proper penetration by forming close coils around the leaf, and so binding host and parasite together. Even here the leaf may yield somewhat to the haustorial growth pressure.

Where the host bark is thin, penetration takes place in these species of the parasite within a few days, and in about a week the apex of the haustorium may be well on its way through the phloem. The haustorium once within the host, tissues develop rapidly, and when penetration is secured the first two small green leaves of the seedling appear. The larger leaves never develop until the haustorial apex has made contact with the vessels of the host, and supplies of water and salts are available.

In some of the experiments, seeds were germinated upon various common hosts of the parasite, others were germinated upon *Dombeya*, *Pittosporum*, and *Sterculia*, plants upon which I have never found any species of *Loranthus* growing in nature. The seeds on the latter hosts germinated and began to penetrate the host's bark in the same time as others growing upon *Eucalyptus*, *Casuarina*, and *Acacia*, etc., but in no case did the haustoria pass beyond the cortex, although food was still present in considerable quantities in the endosperm and even in the haustorium itself. On examining the host's cells, large numbers of crystals of CaC_2O_4 were found in *Dombeya* and *Sterculia*, and large drops of an oily pungent smelling fluid in those of *Pittosporum*. Probably these substances are injurious to the haustorium of *Loranthus*, as the latex of some plants

is injurious to the haustorial development of *Cassytha*. At any rate, not one of the seedlings succeeded in penetrating as far as the xylem tissues of the host, while seedlings upon *Eucalyptus* and *Acacia* did so in the same time.

Connection between host and parasite

The haustorium penetrates through cortex and phloem into the xylem of the host, although THISELTON-DYER (5) stated that in *Loranthus aphyllus* there is no coalescence of the tissues of the host and parasite. In the xylem the haustorial cells in contact with the vessels differentiate into short reticulate tracheids, connecting up with those in the main part of the root by the differentiation of the intervening cells into tracheids also. The reticulate tracheids of the parasite are applied either to the radial or tangential walls of the vessels of the host. There is no definite direction of penetration in *L. celastroides*, the haustorium not confining itself to medullary rays in order to reach the xylem (fig. 38). The entire phloem along its path in front of it is destroyed, and the haustorium appears as one large massive development of parenchymatous cells with large nuclei, and a central core of tracheids. The pits of the tracheids of the parasite are opposite those of the vessels of the host, while in many cases parenchyma cells of the haustorium were in close contact with the tracheids, and, by developing an osmotic suction, probably assist in maintaining a flow from the vessels of the host to the tracheids of the parasite. There is, therefore, undoubted connection established between the xylem tissues of the host and parasite, and the latter withdraws the raw materials from the host (fig. 37). Is there any direct parasitic connection of the haustorial cells with the phloem of the host? The margins of the haustorium are closely applied to living cells in cortex and phloem. Large masses of these tissues are dissolved during penetration, and their contents probably absorbed by the growing haustorium. There are no sieve tubes in the haustorium; the tracheids are surrounded by elongated parenchyma cells of a cambiform type. The absence of sieve tubes might suggest the absence of complete parasitism. At any rate I have found no evidence of sieve plates between the sieve tubes of the host and the parenchyma

cells of the parasite, as one might expect were regular absorption of food taking place by the parasite. As was pointed out in regard to *Cassytha*, the absence of differentiated sieve plates between the tissues of host and parasite does not entirely preclude food absorption.

In *Arceuthobium* there is a very distinct seasonal difference in the parasite. It has a brief vegetative period, flowering and fruiting, scattering its seeds, and then dying away. The haustorial part is devoid of chlorophyll, and therefore when development begins again in the following season, this must be at the expense of the foods in the host, or those which may be stored in the haustorial tissue, toward the close of vegetative activity. In *L. celastroides* and other species there is no such definite seasonal variation. The plant is evergreen, never being devoid of leaves during life, and therefore always capable of photosynthesis, provided the necessary conditions are present (such as temperature, light, water, CO_2 etc.). There is no period during which it might be dependent absolutely upon the host for food for the development of new leaves or flowers or fruits. It is a much less complete parasite than *Arceuthobium*, and somewhat resembles the European *Viscum* in its "water parasitism."

Secondary roots

From the primary center of infection (text fig. 4), characterized in this species by a swollen knoblike development at and around the point where the first root penetrated the host stem (figs. 34–36), a large number of branches are produced which grow out through the cortex of the host from the parasitic parenchyma. These branches are at first reddish in color, the leaves being typically so, as in a great many Australian xerophytes, the reddish pigment in the cells probably having a protective influence from strong insolation while the leaves are young. From this knotlike growth upon the host stem one or more secondary roots arise, which grow out through the cortex and along the host branch. These young roots are characterized by a reddish color similar to the stems and leaves, and even in the old roots the apex remains reddish, while the remainder beneath the loose corky covering has a considerable amount of

chlorophyll present in the cortex. These secondary roots, like the primary, are not sensitive to gravity, growing either up or down the branch with equal readiness. They are sensitive to light, however, and generally grow along the shaded side or on the lower surface of a branch. In such positions these negatively phototropic roots receive the utmost protection from direct light.

Where these roots arise from the upper surface of the host branch, they grow in a loose spiral around the stem, sometimes extending from the upper branches of the host toward the trunk and down it toward the ground. There is evident in such roots,

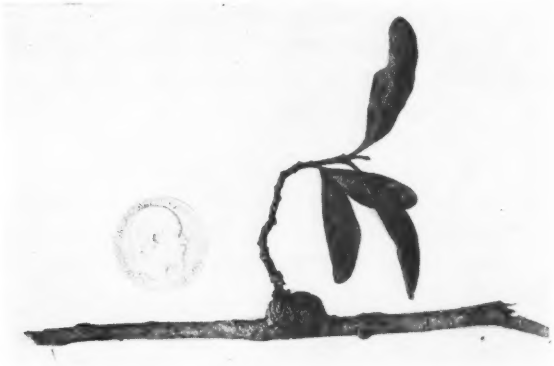

FIG. 4.—Knoblike swellings of parasite upon the host.

especially when produced from the upper region of the swollen part of the host, a form of growth in a loose spiral manner. This is especially evident in shaded localities, where the direct sun's rays do not (or only very infrequently) fall upon the roots. When the original center of infection is situated high up in the host's branches for purposes of floral display and pollination, these secondary roots grow downward toward the main trunk, always in a loose spiral direction of growth. This peculiar spiral growth is somewhat unusual in roots, and it very strongly suggests circumnutation in aerial shoots, and especially in climbing stems. I have observed numerous instances of such secondary roots, hanging down from the main clump of the parasite or the host stem near it, developing

into a close series of spirals (text figs. 5, 6). These roots are frequently normal in structure, and in many cases branched in the ordinary way. In a few exceptional examples they even develop a small aerial shoot. Growth continues for a very long time,

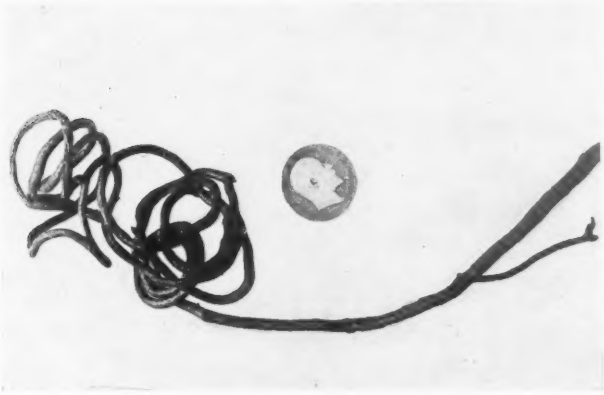

FIG. 5.—Secondary roots.

FIG. 6.—Secondary roots.

some of them attaining a length (when stretched) of 100 cm. In appearance they resemble the coiling of tendrils which have been intermittently stimulated, and developed into a typical series of close coils. The coiling is from left to right. The spirals were invariably close upon these peculiar roots, and more pronounced than in other

roots which grow along and around a branch of the host. Unfortunately, so far I have not been able to obtain young plants of the parasite sufficiently advanced to test the peculiar example of irritability which these roots appear to possess, but I hope on a future occasion to throw some light by means of experimental work upon this phenomenon.

Such roots are not only interesting from this peculiar mode of growth around the host branches, but also from their physiological aspect. At intervals along their length (figs. 35, 36), haustoria are developed which penetrate into the host, and absorb the necessary crude sap. These haustoria, as will be shown later, are rootlike in origin and structure. They invariably arise from the younger parts of the root, before there is any suggestion of periderm development, and from the surface in contact with the host. From the upper surface aerial shoots are developed. Generally speaking, there is a very definite correlation between the distribution of the vegetative shoots and the haustoria, this being particularly noticeable where the number of haustoria is few. I do not consider this relation a purely mechanical necessity for the better support of the foliage, as it occurs in both erect and pendent forms, but rather of physiological import, entailing the maximum amount of crude material with the minimum conduction and expenditure of energy. These secondary roots are merely means of spreading the parasite and increasing the area of infection. By their means a whole tree may become completely overgrown with the parasite from top to bottom, the roots spreading in all directions, but mainly downward from the original center.

When new shoots of the parasite have developed from such "runners" many of them die away, leaving the individuals firmly established and independent. I have frequently cut the roots into segments, each with at least one haustorium firmly imbedded in the host, and in a few weeks' time young vegetative shoots have developed.

Where the parasite has attacked *Banksia latifolia* or *B. serrata*, plants noted for their exceptionally thick and often furrowed bark which makes them very resistant during bush fires, the secondary roots often develop down the grooves. In such a position they

are shaded from the light. When developing on *Eucalyptus*, with fissured or stringy bark, the roots grow beneath the layers of old bark in contact with the youngest zone. In such a position they are developing in complete shade, and their growth is more rapid than in those roots developing on the surface of smooth barked hosts. Furthermore, moisture is retained more readily beneath such layers of bark, and the root, therefore, will be developing under very favorable conditions.

The secondary roots do not always develop from the parenchymatous mass of the haustorium within the cortex of the host, but, especially in young plants, they will arise from the portion of the parasite outside the host branch (fig. 34).

Effect of parasite on host

In the case of *L. celastroides*, one very obvious and striking result of the parasite's presence upon the host is the large knots which appear wherever infection has taken place. These knots may vary from the size of a small marble to that of a tennis ball. In most cases they are developed by the massive haustorial tissue in the cortex and phloem of the host, this being the normal condition. When the parasite grows upon *Banksia serrata* or *B. latifolia*, which naturally have very thick barks, the swellings upon the stem may even be greater and considerably longer. In sections of the stems of these plants, haustorial tissue may be found in rings within the wood, cambial activity during successive seasons having enveloped the inner haustorial tissue. The new wood formed each year, however, is again tapped by a further development of haustorial tissue from that part within the cortex of the host (fig. 38). Moreover, there is considerable destruction of host tissue owing to the penetration and development of the haustorium. This involves cork, cortical parenchyma, phloem, and cambium, which may be completely dissolved along the line of growth of the sucker.

Owing to the lateral expansion of the haustorium from the original center of infection around the circumference of the stem, practically all the sap wood of the host branch may be tapped by the tracheids of the parasitic sucker. When this does occur, and

it is common in nature, the end of the branch dies away for lack of water and solutes from the soil. I have seen some *Casuarina* and *Eucalyptus* almost enveloped with this *Loranthus*, and the tops of every branch dead, owing to its presence. This has a disastrous effect upon the entire tree, as very few new leaves can be formed each year. There is no growth on these younger infected shoots, and when the food in the body becomes exhausted, the tree perishes. The presence of the parasite upon the host has therefore a very injurious effect.

Effect of parasitism upon Loranthus

In every case of parasitism yet studied, there has been demonstrated some degree of reduction of the parasite's body. This reduction is reflected either in the absorbing system, or the photosynthetic organs, or both simultaneously. In *L. celastroides*, reduction is most apparent in the root and in the dimensions of the parasite. The root is always a small structure, which later gives rise to the haustorium or sucker, after the tip has become applied to the host branch. The root has no cap, is devoid of normal root hairs, and is incapable of developing in the soil. Up to the present, I have been quite unsuccessful in attempts to produce a normal autotropic independent form of *Loranthus*. Reduced as the root system undoubtedly may be, it is nevertheless efficient to meet the needs of the parasite, as is apparent from the dense tufts of foliage and masses of flowers and fruit which are developed.

So far as *L. celastroides* and most other species are concerned, there is no obvious reduction in the foliar organs. The leaves of *L. linophyllus*, however, are reduced (figs. 39, 40), terete, and simulate those of the plants on which it is generally parasitic, namely *Melaleuca genistifolia* and *Leptospermum* sp., small shrubby types of the Myrtaceae. The whole body of this species is considerably reduced, the tufts being short and dense as compared with those of *L. celastroides*.

Xerophily of L. celastroides and L. linophyllus

The leaves of the former species are large, those of the latter small, reduction in this case apparently being due to xerophily

rather than to parasitism. The outstanding feature of xerophytes is the development of structural modifications in order to reduce transpiration. The leaf is the main transpiratory organ, and therefore its structure, form, and size are invariably modified in some way. All the hosts of *Loranthus* are xerophytes growing upon the sandstone of New South Wales. Although the rainfall may be heavy at times, it is very intermittent, and frequently for weeks and months no rain falls. This is especially true for the interior of the state. This being so, the host and parasite must conserve their water, and to meet this end the leaves are thick, fleshy, and succulent, the outer epidermal wall highly cutinized on both surfaces, and the stomata sunken (fig. 42). In *L. linophyllus*, also, the leaves are reduced. While there is palisade mesophyll on either surface of *L. celastroides* and other pendulous-leaved types, the center of the leaf is occupied by large oval-shaped cells with few chromatophores and mucilaginous sap. These cells have the capacity of storing water (figs. 41, 42). In *L. celastroides* the leaves are generally covered with waxy powder like that on the leaves of *Strelitzia* or the bloom upon many fruits.

The conditions under which *Loranthus* vegetates and flowers are essentially xerophytic, but rather hydrophytic conditions are required for dissemination and germination. There must be a relatively high humidity. It is conceivable that, were the hosts hydrophytic forms, the parasite would show very considerable differences in foliar structure.

Summary

1. *Loranthus celastroides* is fairly widely distributed in New South Wales, but it is particularly common in the coastal strip between the sea and the mountains.

2. Humid conditions are essential for dissemination and germination of the seed.

3. The seed is not ejected with explosive force as in *Arceuthobium*, but glides out of the fruit through an operculum, and is forced out by the swelling of the gelatinous cells at the base of the seed. Rupture of the operculum may take place suddenly on the fruit striking a branch or object when falling.

4. The fruit is comparatively succulent, and may be attractive to bird life, which probably assists in dissemination.

5. There is a great loss of seeds in *Loranthus*, many hundreds from a single plant not reaching a host.

6. Dissemination generally occurs during a dull, humid day, when the fruits become very turgid, owing to diminished transpiration from the parasite and host.

7. Wind is instrumental in depositing many seeds upon branches of a host.

8. For germination of the seed, an adequate supply of food from the endosperm, moisture, favorable temperature, and light are essential factors.

9. The gelatinous coat of the seed has the faculty of absorbing water, and this is the only source of water to the seedling until its haustorium becomes attached to the xylem tissues of the host.

10. The root is short and is not sensitive to gravitational stimulation. It is sensitive to contact, and the apex becomes club-shaped or developed as a haustorial disc when its growth is resisted by a branch of the host. From the center of the "haustorial disc" the haustorium proper develops into the host. The root is negatively phototropic. The haustorial disc becomes securely attached to the host branch by the partial solution of the epidermal cells of the disc and the host.

11. During the period of penetration of a host by the haustorial apparatus, the embryo is nourished chiefly by the food stored in the endosperm, and mobilized by the enzymes of the cotyledons which remain in the seed for absorption. It seems probable that the disintegration of cells of the host in the path of the haustorium also provides food for the development of the embryo.

12. The haustorium becomes applied to the xylem of the host directly. Reticulate tracheids differentiate in its axial zone, and in contact with the vessels of the host. There are no sieve tubes present in the haustorium, whose tissues are represented by the tracheids, procambial cells, cortex, and epidermis.

13. The penetration of the haustorium is probably the result of pressure and of chemical solution. Crushed cells are always to be seen along the margin of the haustorium, while discoloration of

the host cells in advance of the haustorium indicates chemical action.

14. The exactness of the relation between the tracheids of the parasite and the vessels of the host suggests the strong probability of chemical action dissolving the host cells.

15. At the point of infection of a host branch by the parasitic haustorium, a swelling arises from which secondary roots and branches bearing leaves are developed. The secondary roots develop a new series of haustoria farther along the branch. In many cases the branches of the host are killed by the parasite, owing to the tapping of most of the vascular bundles.

16. Morphologically the haustorium is of root origin, simply being a part of the primary root of the seedling developed as a special haustorial apparatus.

17. In some cases the host endeavors to exclude the haustorium by a very pronounced phellogen activity. This occurs in *Ficus* sp.

18. Lateral expansions of the haustorium may occur in the cortex. The haustorium frequently spreads along the cambial zone. In *Banksia* stems, masses of haustorial tissue occur deeply imbedded in the xylem.

19. *Loranthus celastroides* has thick, fleshy leaves and sunken stomata. Its xerophily is probably the result of a semiparasitic life.

20. The parasite vegetates under xerophytic conditions, but dissemination and germination are possible only under hydrophytic conditions.

I desire to record my sincere thanks to Professor A. A. LAWSON for his helpful suggestions and kindly criticism while the work was in progress.

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EXPLANATION OF PLATES XIV–XVI

FIGS. 1–3.—Fig. 1., rupture of fruit and partial extrusion of gelatinous coated seed; operculum being pushed upward; circular line of dehiscence of fruit shown; natural size; figs. 2, 3, fruit showing operculum and region of dehiscence; ×2.

FIG. 4.—Diagrammatic sketch of fruit in longitudinal section, showing operculum (*op*), dehiscence zone (*deh*), wall of fruit, which is frequently succulent (*w*), compressed mucilaginous cells, which causes the extrusion of the seed (*cmc*), abscis zone at base of fruit (*a*), vascular bundle (*vb*), radiating gelatinous zone (*gz*), endosperm (*e*), and embryo (*em*); ×20.

FIGS. 5–7.—Fig. 5, adhesion of seed to branch; figs. 6, 7, seed as it leaves fruit, showing thick, gelatinous covering, which is instrumental in securing attachment to object; natural size.

FIGS. 8, 9.—Cells of gelatinous coat of seed after dissemination; fig. 8, cell walls normal; fig. 9, walls swollen due to addition of water.

FIG. 10.—Section showing apex of cotyledons abutting firmly against endosperm cells; epidermal layer of cotyledons densely protoplasmic, and apparently digestive in function; endosperm cells in contact with cotyledons generally free from starch (or nearly so); ×200.

FIGS. 11–16.—Germinating seeds of *L. celastroides* showing first root (*r*), which becomes swollen at apex, and develops haustorium and first leaves (*z*); seed gradually shrivels as its food reserves become exhausted; natural size.

FIGS. 17–21.—Germinating seeds, showing club-shaped holdfast which develops on end of root, and first leaves; in fig. 18 central portion of holdfast from which haustorium develops is shown (*H*); natural size.

FIG. 22.—Seedling of *L. celastroides*, showing curvature which hypocotyl may execute to bring root apex against object; natural size.

FIG. 23.—Germinating seed of *L. celastroides*, showing holdfast, and hairs which develop upon it; first leaves are shown; natural size.

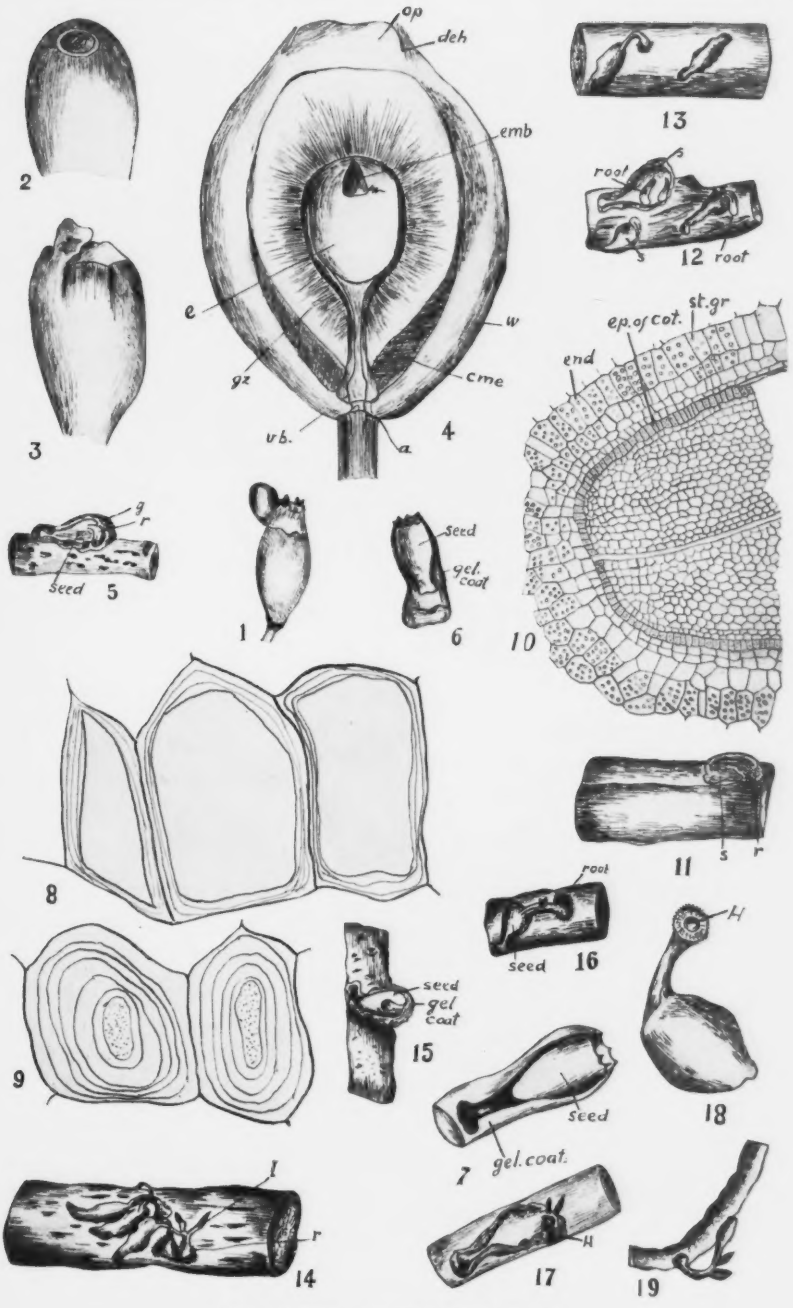
FIG. 24.—Hairs from holdfast of *L. celastroides*, each hair coated with glistening, sticky secretion (*s*), apparently secretory in purpose; ×250.

FIG. 25.—Young hairs from holdfast of *L. celastroides*; ×250.

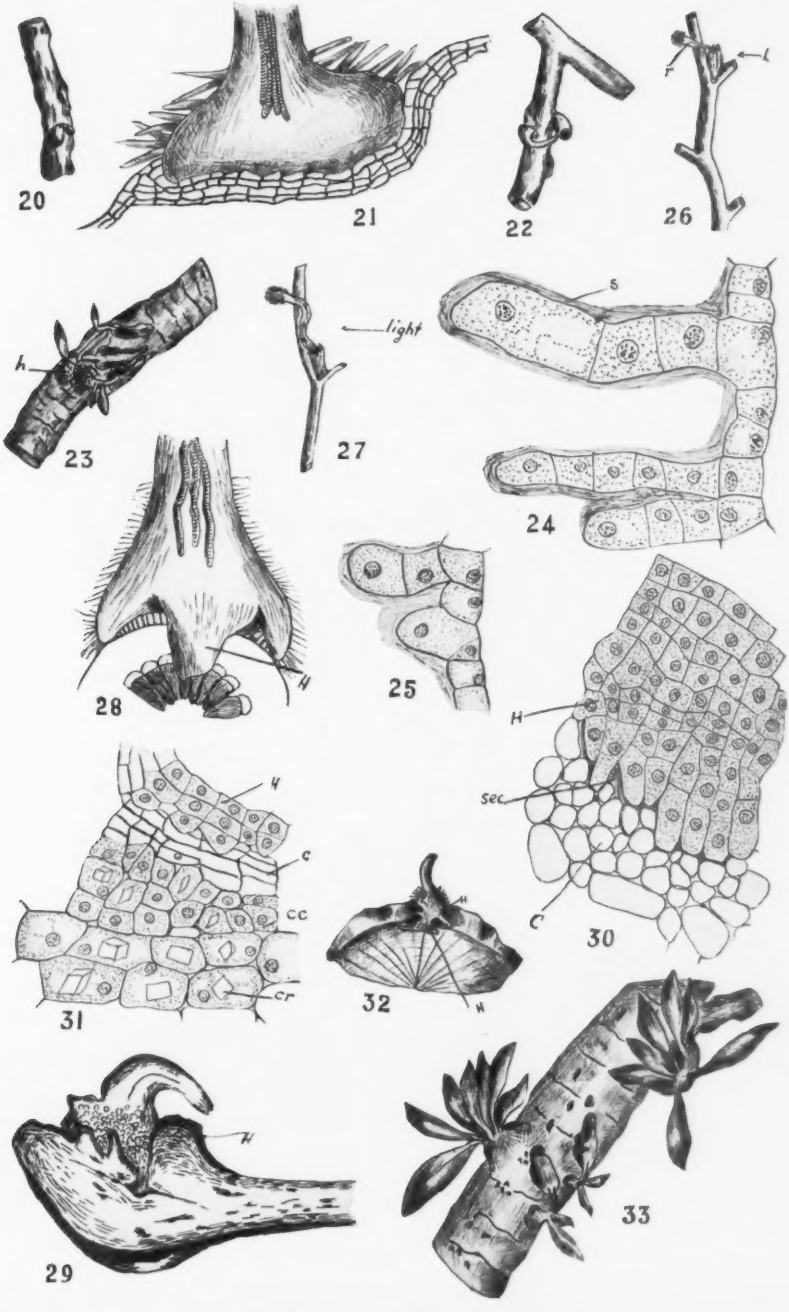
FIGS. 26, 27.—Seedling attached to small plant of *Acacia discolor*, showing curvature of root away from source of light (from right); natural size.

FIGS. 28, 29.—Section of branch of host, showing haustorium of *L. celastroides* imbedded in tissues and in contact with vascular tissue; ×10.

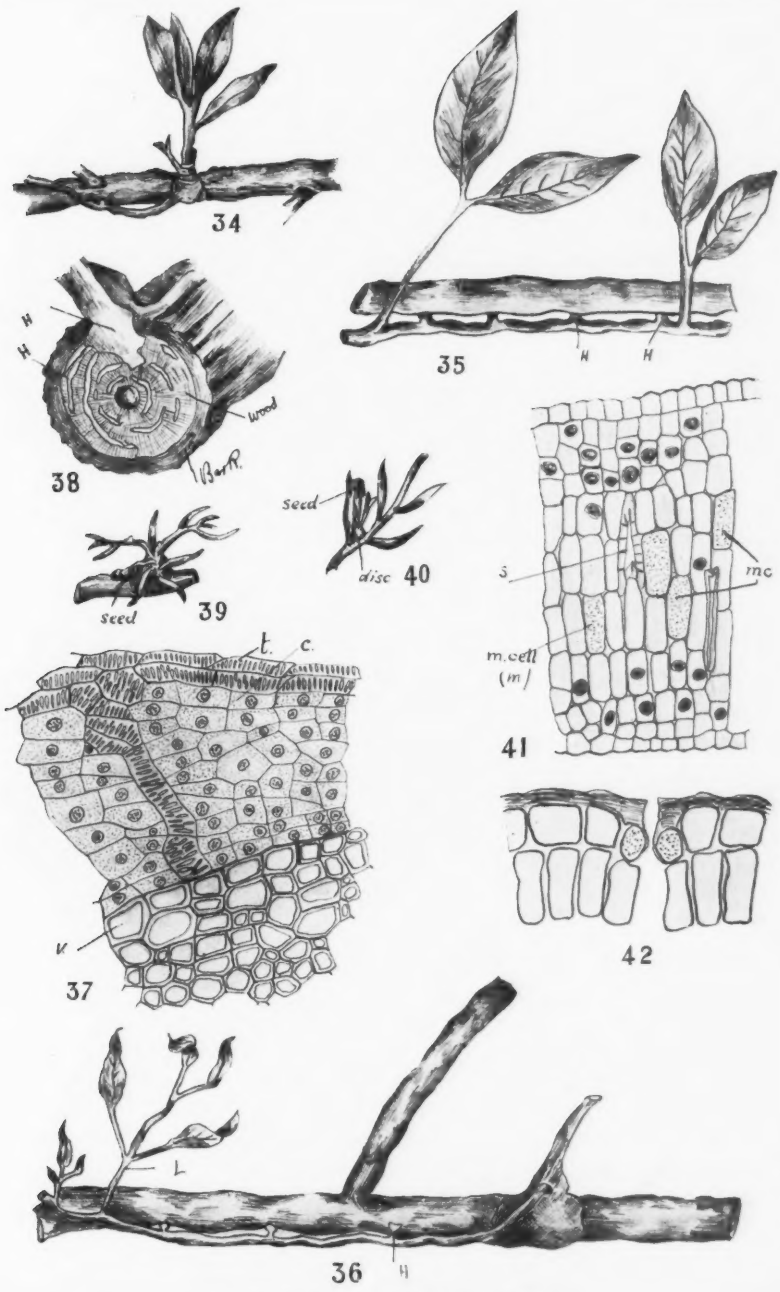
FIG. 30.—Portion of haustorium (*H*) of *L. celastroides* entering cortex (*c*) of host; epidermal cells of haustorium slightly papillate, and secretion emanates from them (*secr*); ×200.



McLUCKIE on LORANTHACEAE



McLUCKIE on LORANTHACEAE



McLUCKIE on LORANTHACEAE

FIG. 31.—Portion of haustorium of *L. celastroides* entering cortex of *Dombeya;* cork cells (*c*) slightly distorted, while cortical cells of host contain calcium oxalate crystals (*cr*); ×200.

FIG. 32.—Transverse section of stem of *Banksia latifolia* with apex of haustorium of *L. celastroides* firmly imbedded in it; haustorium (*H*) is sending out lateral growths through cortex, phloem, and wood of host; natural size.

FIGS. 33, 34.—Host branch becomes swollen where haustorial tissue is developing rapidly; new aerial branches develop from swellings to exterior, bearing later, new leaves and new haustoria; natural size.

FIG. 35.—New secondary roots arise from swellings upon host branches where haustorial tissue is imbedded; natural size.

FIG. 36.—Secondary root with haustoria (*H*) and new foliar shoots (*S*); natural size.

FIG. 37.—Portion of haustorium highly magnified, showing parenchyma cells (*c*) and tracheids (*t*) of which it is composed; latter in contact with vessels (*v*) of host; ×250.

FIG. 38.—Portion of stem of *Banksia latifolia* showing imbedded haustorium of *L. celastroides*, from which narrow lateral growths have developed around and through the wood; natural size.

FIGS. 39, 40.—Plants of *L. linophyllus*, showing small terete leaves; natural size.

FIG. 41.—Transverse section of leaf of *L. celastroides*, showing central water storage tissue which contains mucilaginous sap, large stereids (*s*) also present; ×150.

FIG. 42.—Portion of surface of leaf showing sunken stomata; ×200.

INFLUENCE OF CERTAIN SUGARS ON HIGHER PLANTS[1]

J. M. Brannon

(WITH THREE FIGURES)

It is generally believed that the carbohydrates, quantitatively at least, play a predominant rôle in the metabolism of the plant. In the green plant the sugars commonly found are glucose, fructose, sucrose, and maltose, although the latter if present is in small amounts. Pentoses are undoubtedly widely distributed, and raffinose and other sugars have been noted also. Thus far, however, no adequate data are available with respect to the quantitative distribution of these sugars in plants. Various investigators have given data respecting this phase of the subject, but the inherent deficiencies of the methods of sugar analysis make it difficult to draw any general conclusions with respect to the quantitative distribution of these individual sugars.

Little is known regarding the origin of these four sugars. Maltose apparently is derived from starch; glucose and fructose are produced in the inversion of sucrose, but it is not improbable that the hexose sugars precede the formation of sucrose, and that a hexose sugar is the first sugar produced. There is no evidence as yet as to whether or not glucose or fructose is the first hexose, nor is there any evidence as to whether or not hexose sugars are converted, in the cell, one into the other. It seems reasonable to conclude, however, that in the plant cell glucose may be changed to fructose and fructose to glucose, since conversion has been observed to take place in the laboratory by the use of appropriate methods.

In view of the fact that different sugars are found in the plant, and that the chemical properties of these sugars differ, it seems logical to conclude that each has a different function. Various views on this subject have been advanced, and some investigations

[1] Part of a thesis presented to the Graduate Faculty of Cornell University in partial fulfillment for the degree of Doctor of Philosophy.

made, particularly with respect to glucose and fructose. For example, ARMSTRONG (2) states that fructose is used primarily in tissue production and glucose is used primarily in respiration. This view is adhered to by a number, but the evidence being inconclusive and the results of other investigators being contrary to the idea, it seemed desirable to investigate the subject. This paper, therefore, considers particularly the influence of glucose and fructose on plant growth.

Review of literature

BROWN and MORRIS (3) observed that in *Tropaeolum* the hexoses of the leaf, instead of being present in a proportion corresponding with invert sugar, invariably appeared to consist very largely of fructose. In some cases glucose was entirely absent, in other cases the proportion of fructose to glucose varied from about six to one to about two to one. They concluded that glucose was more rapidly used in respiration than fructose.

LINDET (16) studied the proportion of the hexoses in the leaf and leaf stalk of the sugar beet at different periods of growth. He apparently found that in normally growing leaves, especially in the earlier stages of growth, the amount of glucose was generally slightly greater than that of fructose, although on several occasions fructose was in excess of glucose. On the other hand, in the leaf stalk fructose was invariably found to form only a small proportion of the sugar present. LINDET came to the conclusion that glucose is used largely in respiration, while fructose is used largely in tissue formation. He obtained similar results when he grew barley embryos in Raulin's solution containing sucrose. The plants absorbed glucose more rapidly than fructose.

PARKIN (23) found that fructose was generally in excess of glucose in the leaf of *Galanthus nivalis*, so he concluded that glucose is used more easily in respiration.

COLIN (4) determined the ratio of glucose to fructose in leaves and petioles of etiolated shoots grown from the tuber of the artichoke, and found it to be greater than one in all cases. The reserve carbohydrates of the artichoke and chicory would furnish fructose. In shoots of these plants growing normally, fructose is in excess in

the leaf parenchyma. The proportion of glucose increases on going down the veins and petioles. In the latter the amount of glucose finally exceeds the fructose. According to COLIN, respiration is less intense in etiolated leaves than in green leaves. He thinks that fructose is used more rapidly in tissue building than glucose, and that the latter is used in respiration, and therefore there is an excess of the latter in etiolated leaves.

DAVIS, DAISH, and SAWYER (8) found that in the mangold leaf glucose always seemed to be in excess of the fructose, especially in the midribs and stalks; whereas in the potato, DAVIS and SAWYER (9) found fructose apparently predominating over glucose. These investigators think that glucose and fructose are present in nearly equal amounts, as they should be if they were formed by the inversion of sucrose. DAVIS (7) states that in the mangold leaves and stalks, optically active impurities are always present which are not precipitated by basic lead acetate, as follows:

> These substances are possibly acid amides (such as glutamine and asparagin) or amino-acids (such as glutamic and asparatic acid) which form soluble lead salts. . . . . The apparent fluctuations in the ratio of dextrose to levulose are probably due to fluctuations in the optically active impurities rather than variations in the sugars themselves. This is shown by the fact that these fluctuations can be correlated with the differences between the cane sugar values as determined by reduction and polarization. When the apparent dextrose increases faster than levulose increases, the results for cane sugar obtained by polarization are lower than the reduction values. When the apparent dextrose increases faster than the levulose or the levulose falls more rapidly than dextrose, the polarization results are in excess of the true values.

DAVIS thinks that there is a regularity in the variations of the optically active impurities. In the light of these observations, it is difficult to accept as valid the conclusions of other workers with respect to the ratios of glucose to fructose. As will be pointed out, no very comprehensive experiments have yet been made to determine the relative influence of each of these two sugars on plants.

MOLLIARD (22) states that fructose up to 10 per cent increases the growth of radish grown on agar in tubes to a greater extent than does glucose. Furthermore, the glucose-fed plants tend to yellow, which is not the case with those supplied with the lower concentration of fructose. He found that the growth was very

much reduced with 15 per cent fructose, the plants produced being quite abnormal. With 15 per cent glucose, on the contrary, the plants were well developed. Apparently the two sugars influence the growth differently.

SERVETTAZ (**27**), in comparing the influence of certain sugars on the growth of *Hypnum purum*, found that glucose and fructose at a concentration of 0.5 per cent influenced growth in the same way and were used in approximately the same amounts.

In his experiments with *Ceratodon purpureus*, ROBBINS (**24**) found that with cultures grown in the light, the dry weight of the moss supplied with fructose was 63.4 mg., while when supplied with glucose the weight was only 34.5 mg. When grown in the dark the yield of dry matter with fructose was approximately seven times as great as that when glucose was furnished, the weights being with fructose 85.4 mg. and with glucose only 11.5 mg. The amount of sugar consumed was correspondingly greater in the fructose culture than in the glucose cultures. The striking difference between the results reported by SERVETTAZ and ROBBINS may be due to the fact that the nutrient solutions used by each were markedly different.

MAIGE and NICOLAS (**20**) made a study of the absorption of various sugars and the influence of these on respiration, as measured by the production of CO_2 and the absorption of oxygen. For this purpose etiolated buds of a bean were used. A uniform lot of each was immersed for approximately 24 hours in 10 per cent solution of sucrose, maltose, lactose, glucose, or fructose. Considering the two latter sugars, the data indicate that the glucose was absorbed to a greater amount than the fructose. Likewise the glucose-supplied tissues showed in respiration experiments a greater consumption of oxygen and greater evolution of carbon dioxide. The increased respiratory rate with glucose may have been due to the fact that a greater quantity of that sugar had been absorbed. It is possible also that the greater amount of glucose was absorbed, not because of a greater permeability of the tissues for glucose, as is suggested by them, but because the glucose was more readily transformed into starch or more easily katabolized during the period of absorption.

KNUDSON (10) found no very appreciable differences in the use of glucose and fructose by corn grown either in the light or dark. Glucose seemed to be slightly more favorable, however, although fructose-fed plants attained a greater length. In experiments on the nonsymbiotic germination of orchid seed, the same worker (14) found marked differences in the effects of glucose and fructose on germination, the latter sugar being more favorable.

From the foregoing review of the literature, it is apparent that these sugars do not function in the same way. For this reason, it was decided to make an investigation of the influence of these two sugars on plants, and attempt to determine whether or not one or the other sugar was more favorable for tissue formation. It was the hope that one of the sugars might influence the growth in marked contrast with the other. Such results might conceivably be of value in the interpretation of certain plant responses, and might be of value in the propagation of plants, especially cuttings of plants that are difficult to propagate. The results here reported are not as conclusive as one might wish, but nevertheless some rather striking facts are brought out with respect to the influence of these two sugars on plant growth.

Methods

The plants used in these experiments were *Pisum sativum*, *Medicago sativa*, *Raphanus sativus*, *Phleum pratense*, and *Bryophyllum*. The seeds from which these plants grew were sterilized by the calcium hypochlorite method of WILSON (28). In case of the *Bryophyllum*, small portions of the leaves were cut from the leaves of a large plant with a pair of sharp scissors. These pieces of leaves were first immersed in 95 per cent alcohol and then immersed into a 1–1000 bichloride solution for 50 seconds. All the experiments were conducted in the greenhouse, but under conditions of darkness. The cultures were placed in a box so constructed that there was proper circulation of air. The inside of this box was painted black, and all other precautions were taken to make it lightproof. The culture solution used was Pfeffer's as used by KNUDSON (10). The sugars used were all of a very high degree of purity.

After sterilizing, the seeds were sown directly into the culture solution, using all precautionary methods to prevent contamination.

FIG. 1.—1, pea plant grown in Pfeffer's solution minus sugars; 2, pea plant grown in Pfeffer's solution plus fructose (note root system); 3, pea plant grown in Pfeffer's solution plus glucose.

By the method employed, germination of the seed occurs when it is immersed in the culture solution, and it is only after a period of

growth that the stem grows above the surface of the solution. The method which has already been described has the advantage that the absorption takes place not only by means of the roots, but also by the stem. This permits of a more rapid growth than when absorption is merely by the roots, a condition which parallels the observation of AQUA and JACOBACA (1) that sugar absorbed by the cut

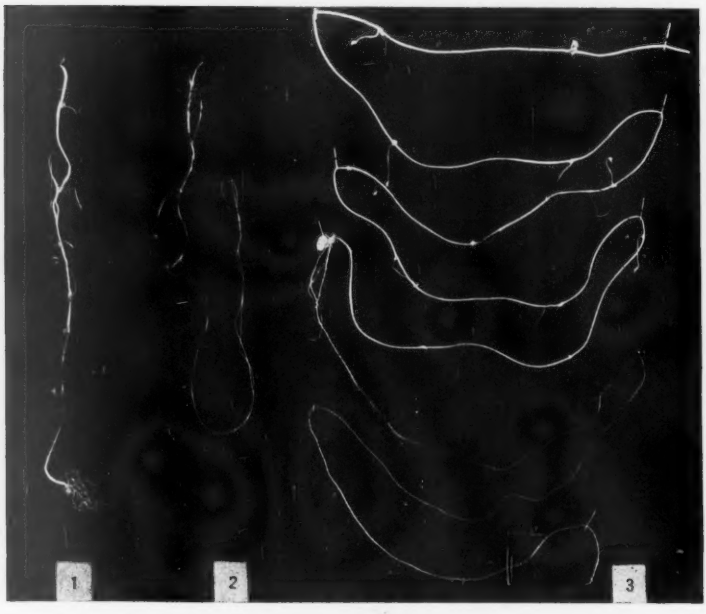


FIG. 2.—1, pea plant grown in Pfeffer's solution plus fructose; 2, pea plant grown in Pfeffer's solution alone; 3, pea plant grown in Pfeffer's solution plus glucose.

surface of the leaf permits of a more active growth than if absorption is entirely by the roots.

Experiments

EXPERIMENT I.—One seed of *Pisum sativum* was sown in each culture vessel, which in each case was an Erlenmeyer flask of one liter capacity, and the amount of the culture solution used in each flask was 100 cc. In the glucose-containing solution the plants grew very well. In two cases the stem grew between the

cotton stopper and flask and made a considerable growth outside the flask. An interesting fact with respect to these two plants is that they produced rudimentary flowers, which, however, became

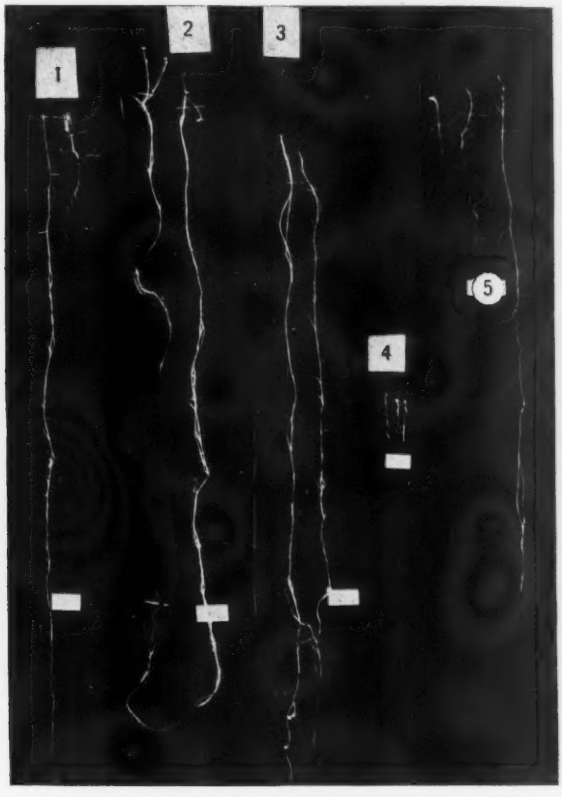


FIG. 3.—Representative alfalfa plants grown in solutions containing sugars: 1, Pfeffer's solution containing maltose, 2, Pfeffer's solution containing sucrose; 3, Pfeffer's solution containing glucose; 4, Pfeffer's solution minus sugars; 5, Pfeffer's solution containing fructose.

abscissed in the course of a few days. In the fructose-containing solution the seeds germinated, but only a few grew. Fructose is apparently toxic to the seedlings, for out of the six cultures only two plants were obtained, the remaining four not going beyond the

relatively early stages of germination. In all these cases the early roots produced were killed. The two plants in fructose cultures made most of their growth during the last six weeks of the experiment. The interesting point is here brought out of the toxic effect of a sugar being evident at one stage of growth and not at another. KNUDSON (11) found a similar case in studying the toxicity of galactose. The data show that in Pfeffer's there was a marked loss in weight while in the glucose cultures, the plants either gaining

TABLE I

INFLUENCE OF GLUCOSE AND FRUCTOSE ON *Pisum sativum* DURING TEST OF FOUR MONTHS

Original dry weight of seed (mg.)	Dry weight of residual cotyledons (mg.)	Total dry weight of plant (mg.)	Loss or gain (mg.)	Length of stem (cm.)	Length of root (cm.)
	Pfeffer's+2 per cent glucose				
390.9.....	122.5	432.6	+41.7	150	39
367.3.....	117.5	324.6	−42.7	60	6*
347.0.....	105.0	332.4	−14.6	90	32
418.9.....	159.5	515.0	+96.1	90	48
	Pfeffer's+2 per cent fructose				
374.1.....	183.2	332.5	−41.6	18	20
337.0.....	162.9	308.6	−28.4	15	10
	Pfeffer's solution				
417.5.....	.....	212.6	−204.9	10	9
510.7.....	76.4	309.0	−201.7	.....	.....
417.5.....	122.1	151.3	−266.3	32	23
365.3.....	98.2	98.2	−267.1	33	40

* Roots much branched.

or showing a slight loss in weight, while with the two fructose cultures there was only a slight loss. It will be noted that in the fructose cultures the dry weight of residual cotyledons was greater than in case of glucose cultures.

EXPERIMENT II.—The results of experiment I, showing the toxicity of fructose, were so unexpected that the experiment was repeated. The amount of sugar used was also determined. In the glucose cultures, five out of nine plants showed a definite increase in dry weight, while three showed a loss. In the fructose

cultures, five out of six showed an increase, while only one showed a loss. This at first would suggest that fructose is more favorable than glucose, but the greater weight is due, very largely, to the fact that the plants of the fructose cultures made very little growth.

TABLE II

INFLUENCE OF GLUCOSE OR FRUCTOSE ON GROWTH OF *Pisum sativum;* SEEDS PLANTED SEPTEMBER 31, 1920; NOTES TAKEN FEBRUARY 23, 1921*

Original dry weight of seed (mg.)	Dry weight of plant (mg.)	Gain or loss (mg.)	Sugar used (mg.)
	Pfeffer's+2 per cent glucose		
177	198	+21	.....
317	319	+ 2	1206
237	212	−25	1130
234	152	−82	478
201	201	0	1042
233	202	−31	972
173	236	+63	1866
156	162	+ 4	1042
182	197	+15	.....
	Pfeffer's+2 per cent fructose		
259	337	+78	1691
208	162	−46	.....
271	344	+73	1733
215	323	+108	2000
200	206	+ 6	958
197	214	+17	1189
	Pfeffer's solution		
222	85	−137	.....
184	66	−118	.....
153	72	− 81	.....
225	101	−124	.....
180	78	−102	.....

*Amount in check flask, glucose 1316 mg., fructose 2044 mg. Average dry weight produced in flasks containing (1) glucose, 212 mg.; (2) fructose, 284.8 mg.; (3) Pfeffer's, 80.4 mg. Average amount used, glucose 1105 mg., fructose, 1514 mg. Amount per milligram dry weight produced, glucose 5.3, fructose 5.4.

The development of the main stem was the same with glucose and fructose, but with glucose the roots attained a length of 40–90 cm. and were much branched, while with fructose the roots were only 5–15 cm. in length, and the lateral roots were very short.

Furthermore, out of twelve seeds planted in the fructose solution only six developed plants. The remaining six seeds germinated only to the extent of the emergence of the hypocotyl. Fructose is toxic not only to the seed, preventing development, but is also toxic to the roots.

If we calculate the amount of sugar used per milligram of dry weight, we find that the average amount of glucose used is 5.4 mg., while for the fructose it is 5.3 mg. The data do not suggest that one sugar is used primarily for tissue formation and the other in respiration; the only significant fact brought out is that fructose is toxic. This point has been suggested in a recent paper by ROBBINS (**25**).

EXPERIMENT III.—In this experiment alfalfa was used and grown in culture flasks containing 100 cc. of the nutrient solution. The sugars used were glucose, fructose, sucrose, and maltose. All cultures were maintained in the dark chamber and the duration

TABLE III

INFLUENCE OF CERTAIN SUGARS ON ALFALFA DURING TEST OF SEVEN MONTHS; AVERAGE DRY WEIGHT OF SEED, 2.4 MG.

Culture solution	Number of cultures	Total number of plants	Average dry weight per plant (mg.)
Pfeffer's+1 per cent glucose	22	160	17.3
Pfeffer's+1 per cent fructose	3	22	24.3
Pfeffer's+1 per cent sucrose	9	99	15.9
Pfeffer's+1 per cent maltose	16	155	12.9
Pfeffer's solution	7	56	1.1

of the experiment was seven months. Table III summarizes the data of this experiment.

The average weight for the plants in the levulose culture cannot be given much consideration, as only three cultures were included in the final data, and the average weight of each was 15, 18.8, and 39.1 mg. respectively. There were originally set up fifteen cultures, but in twelve of them the seeds merely germinated and made no further development. Under the conditions of the experiment fructose apparently is injurious to the young embryo, or else it inhibits digestive processes in the cotyledons which are necessary

for growth. It will be recalled that a similar condition was noted in experiment I. Sucrose is not at all injurious, and since it is probably hydrolyzed in the plant yielding initially glucose and fructose, it would appear that in some way the glucose antidotes the toxicity of fructose. A preliminary experiment with pea suggests this to be the case. The interesting fact is brought out that alfalfa when supplied with sugar and maintained in the dark may show a considerable increase over the weight of the seed.

TABLE IV

INFLUENCE OF GLUCOSE AND FRUCTOSE ON RADISH DURING TEST OF SIX MONTHS (FEBRUARY 2–AUGUST 2); AVERAGE WEIGHT OF SEED, 13.4 MG.

PFEFFER'S+2 PER CENT GLUCOSE		PFEFFER'S+2 PER CENT FRUCTOSE	
Dry weight of plant (mg.)	Amount of sugar used (mg.)	Dry weight of plant (mg.)	Amount of sugar used (mg.)
132	1809	102	1797
181	1900	214	1940
246	1900	200	1950
172	1794	151	1838
183	1900	128	1929
208	1817	238	1950
183	1900	.....	.....
130	1784	.....	.....
179	1945	.....	.....
Av.: 179±7.9	1861±13.28	172±14.6	1901±18.2

In certain individual cultures the increase was as high as seventeen-fold.

The plants grown in the cultures containing maltose present some peculiarities. They were nearly all short, relatively thick, and brittle, and rusty in appearance. When a plant did grow to any length, the stem had black spots at the points where branches would be expected. Still the weight per plant was about equal to that of plants growing in solutions containing either dextrose or sucrose. Examinations of cross-sections of the stems of the plants grown in the cultures containing maltose showed that the cortex and pith were completely filled with starch. Not a trace of starch could be found in sections of the stems of the plants grown in solutions containing any of the other sugars used in this experiment.

Evidently the enzyme maltase is not present in the stem of the alfalfa in sufficient amounts to digest maltose, or if present it does not function. Another explanation that might be offered is that

TABLE V

INFLUENCE OF GLUCOSE AND FRUCTOSE ON TIMOTHY DURING TEST FROM JANUARY 5 TO APRIL 1; FRUCTOSE CONCENTRATION, 898.5 MG. PER 100 CC.; GLUCOSE CONCENTRATION, 876.5 MG. PER 100 CC.

Culture solution and number	Number of plants	Original dry weight of seeds (mg.)	Total dry weight of plants (mg.)	Gain over seed (mg.)	Total sugar used per plant (mg.)	Average dry weight per plant (mg.)	Sugar used per mg. dry weight
	Fructose						
1	33	9.4	73.0	63.6	134.9	2.21	1.85
2	24	6.8	44.0	37.2	52.9	1.83	1.20
3	28	8.0	101.0	93.0	186.9	3.60	1.85
4	59	16.9	98.3	81.4	176.5	1.66	1.79
5	57	16.3	119.4	103.1	233.3	2.09	1.95
6	58	16.6	102.1	85.5	180.1	1.76	1.76
7	55	15.7	147.1	132.0	268.1	2.68	1.81
8	64	18.3	149.0	130.7	272.9	2.33	1.89
9	52	14.9	72.0	57.1	153.3	1.38	2.13
10	34	9.7	47.2	37.5	106.1	1.39	2.25
11	40	11.4	57.9	46.5	110.5	1.45	1.90
12	36	10.3	63.2	52.9	109.7	1.75	1.73
13	29	8.3	74.9	66.6	158.5	2.58	2.11
	Glucose						
1	43	12.3	51.0	38.7	72.9	1.18	1.43
2	43	12.3	64.0	51.7	75.7	1.48	1.18
3	39	11.1	23.0	11.9	18.5	0.59	1.55
4	37	10.6	83.9	73.3	159.3	2.26	1.78
5	38	11.1	110.7	99.6	216.5	2.84	1.95
6	38	10.9	29.0	18.1	51.3	0.76	1.77
7	33	9.4	72.0	62.6	128.1	2.18	1.78
	Averages (results)						
Fructose	44	12.5	85.4	76±5.9	164.9	2.05±0.11	1.86±0.04
Glucose	39	11.1	57.6	50±7.8	102.3	1.61±0.21	1.63±0.06
No sugar	46	13.1	6.6	6.5*	.....	0.14	.....

* Loss.

either maltose or a substance produced from maltose inhibits growth, with the result that maltose is converted to starch. In support of the first of these possibilities is an observation of ROBERTSON, IRWIN, and DODSON (**26**), who show that maltase is present in the leaves and roots of *Beta vulgaris*, but not in the stem.

EXPERIMENT IV.—The culture methods were the same as used in the preceding experiment. Radish proved to be a good plant for this kind of work. It grew well and the leaves were more nearly like those that are formed in the light. In the cultures of pea and alfalfa the leaves were quite rudimentary. Neither glucose nor fructose is toxic to radish, and the data in table IV indicate that both are equally well used.

TABLE VI

Bryophyllum GROWN IN DARK IN PFEFFER'S SOLUTION CONTAINING EITHER GLUCOSE, FRUCTOSE, SUCROSE, OR MALTOSE DURING TEST OF ELEVEN MONTHS

Sugar used	Dry weight produced	Length of stem (cm.)	Length of root (cm.)
Glucose	0.0023	7	4
Glucose	0.0056	9.5	5
Glucose	0.0053	8.5 3.5	6
Glucose	0.0094	7 12	4
Glucose	0.0221	6.5	6.5
Fructose	0.0005	5	0
Fructose		2	0
Sucrose	0.0022	5	4.5
Sucrose	0.0043	6	3
Sucrose	0.0058	6	4
Sucrose	0.0054	2 4	6
Sucrose	0.0056	9.5	3
Sucrose	0.0068	5	3
Maltose	0.0027	5	2
Check	0.0022	4	1
Check		3.5	1.5
Check		3	2

EXPERIMENT V.—In this experiment timothy was grown in the usual way. The detailed data and a resumé are presented in table V. The experiment shows that under the given conditions, fructose is of more value than is glucose when growth of the plant is considered. The dry weight of those plants supplied with fructose is greater than of those furnished with glucose. It is interesting to note, also, that the amount of sugar consumed per milligram of dry weight is greater for the fructose than for the glucose culture. This suggests that fructose is more easily used in respiration than is glucose.

EXPERIMENT VI.—This experiment was performed with cuttings from *Bryophyllum*. Six cultures were prepared with each sugar. These were sterilized, as previously described, in alcohol and mercuric chloride. The experiment lasted eleven months. The plants in glucose made their best growth during the last of the eighth month and early part of the ninth. The greatest dryweights were produced by the plants grown in the solution containing either glucose or sucrose. Most of the pieces of the leaves planted in maltose and fructose produced no plants. The two produced in the solution containing fructose had no roots, due probably to the toxicity of fructose.

Discussion

This investigation was started with the purpose of determining whether glucose or fructose was the better tissue former. The results secured do not give a definite answer. The data indicate that different kinds of plants differ as to the sugar they are able to use most efficiently. Alfalfa grows best in solutions containing glucose, while timothy seems to do better in solutions containing fructose. The pea, when it escapes the toxicity of fructose, does as well on fructose as on glucose. The radish uses both sugars equally well. The probability is that when the whole plant kingdom is considered, no general statement can be made. From the data of other investigators on organic nutrition of higher plants and that presented here, it would seem that all plants can use glucose in some degree. This same statement can be made for sucrose; while galactose, mannose, and fructose have been shown to be toxic to some plants. Maltose has never been shown to be toxic to any plant, but when the alfalfa grown under the conditions of these experiments absorbed maltose, it did not utilize it.

The evidence which led BROWN and MORRIS (3), PARKIN (23), and COLIN (4) to conclude that glucose is used largely in respiration, while fructose is used largely in tissue formation, has been presented in the literature review. This evidence is indirect. DAVIS (6) has criticized the evidence of these investigators, and has pointed out that as yet there are no methods which can be relied upon to distinguish between glucose, fructose, and other substances found

in plants. Part of LINDET's evidence is also subject to this criticism. He has published direct evidence that fructose is used more than glucose in tissue formation. He grew higher plants on Raulins' solution containing either glucose or fructose, and found that fructose produced the better growth. On the other hand, KNUDSON (10), working with various species of higher plants and with various sugars under many different conditions, found no evidence that fructose was superior to any other as a tissue former. ROBBINS' (24) work with the moss is also evidence of a direct nature. Figs. 4 and 5 in his publication show that *Ceratodon purpureus* produced a much better growth on fructose than on glucose, but a survey of the data published by SERVETTAZ (27) indicated that the mosses with which he worked utilized glucose and fructose alike.

The manner in which animals utilize glucose and fructose is not without interest here. LEVENE and MEYER (15) found that the kidney acts on fructose, glucose, and mannose, producing the same d-lactic acid. The percentage of loss of sugars in all cases was about the same. LUSK (17) points out that a fasting rabbit can form glycogen from fructose prepared from inulin. MANDEL and LUSK gave a phlorizinized dog lactic acid and found that it was eliminated as glucose. There is no evidence that fructose is ever formed in the animal from lactic acid. LUSK states, "Isaac perfused a fluid made up of washed dog's blood-cells and Ringer's solution containing fructose through the liver of a fasting dog and found that fructose was converted into glucose." ISHIMONI found that glycogen is deposited in the liver after the intravenous injection of glucose and fructose. The rise in the carbon dioxide output is greater after fructose has been taken by animals than after glucose has been taken. This is thought to be due to the fact that fructose is less readily retained in the liver as glycogen, and so reaches the tissues in greater amounts than does glucose.

DURIG gave 100 gm. of glucose to a man and compared the metabolism with that obtained after giving 100 gm. of fructose. The heat production as measured by indirect calorimetry was 10 per cent higher with fructose than with glucose. The respiration quotients were frequently over unity, thus indicating that fructose is more readily converted into fat than glucose. LUSK has proved

that when 12.5 gm. of glycocoll, which are convertible into 10 grams of glucose, are given to a phlorizinized dog, the heat production is largely increased. Not so, however, with fructose. When 10 gm. of glucose are given to a phlorizinized dog, there is no increase whatever in metabolism. The chemical intermediates between fructose and glucose are without stimulating influence. The point of this quotation is that when an animal is diabetic, a condition which occurs in phlorizinized animals, practically all sugars are converted into glucose.

What the intermediate changes are which one sugar passes through when being converted into another sugar by a living organism is not known. In the laboratory, glucose is converted into fructose by first forming an osone and then by careful reduction fructose is formed. D-glucose, d-mannose, and d-levulose have the same molecular configuration excepting in the first two carbon atoms. According to NEF, if any of these sugars is dissolved in weak alkali and then allowed to stand, all three sugars will appear in the solution. This is probably due to a common enolic form which is produced under these conditions. It is possible that much of the effect of sugars on metabolism is due to the unstable enols. It may be pointed out here that, while fructose can be converted into glucose in the animal, the reverse process apparently never takes place. All the evidence we have indicates that the animal would use glucose rather than fructose in tissue formation, while fructose, when present, seems to have the greater effect on respiration.

From a survey of all the data obtainable on higher plants in the literature, it seems apparent that most of the evidence is against the view that fructose is more serviceable as a tissue former than glucose. The data also seem to favor the view that if either sugar is more readily used in respiration, it is fructose. It is known that fructose is the more unstable of the two sugars. MATHEWS (18) has shown that in alkaline solutions fructose is oxidized nearly four times faster than glucose. Also, if his depolarization theory holds true, fructose (or its metabolic products) is not only more readily oxidized, but aids anaerobic respiration by combining with the hydrogen of other compounds, thus freeing the oxygen to be utilized in respiration.

The materials which a plant will use in its nutrition vary somewhat with the conditions under which it is growing. This is well illustrated by KNUDSON'S results with timothy. When this plant was grown in the light, it would not use lactose as a source of carbon, but when grown in the dark it did use this sugar. The writer knows of no experiment to show whether the plant, like the animal, tends to convert fructose into glucose after it has been absorbed.

Before any definite conclusions can be arrived at in connection with this problem or any allied problems, more will have to be known about the intermediary metabolism of plants.

Summary

Excepting in the case of the timothy, the data presented here do not support the theory that fructose is superior to glucose as a tissue former.

Fructose under the conditions of these experiments has a tendency to be toxic to the roots of pea, alfalfa, and *Bryophyllum*. In some cases this toxicity is temporary. When the two sugars are in the same solution there is no injurious effect to the pea. The pea, alfalfa, radish, and timothy can greatly increase their dry weights when grown in the dark on nutrient solutions containing these sugars. In one or two instances there was an increase of nearly ten times the weight of the seeds sown.

The writer wishes to acknowledge his indebtedness to Professor LEWIS KNUDSON for many suggestions given during the course of this work, and for aid in preparing the manuscript; and also to Dr. E. F. ARTSCHWAGER who took the photographs.

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A PALEOZOIC ANGIOSPERM FROM AN AMERICAN COAL BALL

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **305**

J. HOBART HOSKINS

(WITH PLATE XVII AND SEVEN FIGURES)

Calcareous masses in coal seams containing sectionable plant material have been recognized in Europe since 1854, when HOOKER and BINNEY (4) gave a definite account of the presence of them in coal seams of Lancashire, England, and suggested that the immediate cause of the calcification of the plants was due to the abundance of fossil shells in the shales immediately overlying the coal seams. While these coal balls have been found in large numbers in the Carboniferous coal beds not only of England, but also on the continent, especially in France and to a small extent in the coal fields of the Ostrau-Karwin basin in Moravia, the extensive American Carboniferous had failed to produce them until they were found by Dr. A. C. NOÉ (6) in the summer of 1922, as a result of a definite search for them extending over a considerable period of time and involving personal examination of many mines and coal seams. Dr. NOÉ now has collected numerous coal balls from a number of mines representing different coal seams in the states of Illinois and Kentucky. Through his generosity, and under his direction, the writer has had the privilege of cutting many of these coal balls, and all those sectioned have shown preserved plant tissue. Pyrite is generally present in all the balls sectioned thus far, varying from a negligible quantity to an amount so large that sectioning is impracticable.

In sectioning one of these coal balls, a stem of evident monocotyledonous affinities was discovered. Hitherto the oldest angiosperms showing structure have been five genera of dicotyledons of one species each, described by STOPES (8) from the Aptian or Lower Greensand of Belfordshire, England. CHAMBERLIN and SALISBURY (2) place the Aptian as the upper formation of the

Comanchean or Lower Cretaceous. Of these earliest dicotyledons STOPES (8) states that "though these specimens have a peculiar interest, as they are the oldest dicotyledons of which the anatomy is known, from any part of the world, they are not in any sense 'pro-angiospermic,' and the really primitive forms are still awaited."

Angiosperms, both monocotyledons and dicotyledons, have been described from impressions from earlier formations, and while many of those formerly classified as angiosperms from the lowest formations of the Comanchean have since been questioned and in many instances definitely shown to be gymnosperms or pteridophytes, they form, according to BERRY (1), 35 per cent of the Albian flora of Portugal, and are undoubtedly present in the Urgonian of Greenland. In the latter case, however, their age is not beyond question and they may be younger. By the close of the Cretaceous, however, the angiospermic flora was the dominant one, possessing quite a modern aspect. As a result of this sudden appearance of a large and relatively modern angiosperm flora in the Cretaceous, which has been the subject of much speculation as to origin, a long period of development previous to the Cretaceous has been held necessary by some, who are prepared for an announcement of an older angiospermic flora.

The coal ball from which the sections were made with which this paper deals was collected from the O'Gara mine no. 9, coal seam no. 5, near Harrisburg, Illinois, by the Illinois State Geological Survey. It was recognized and identified by Dr. NOÉ, to whom it was kindly given, and who, in turn, generously gave the writer the privilege of being the first to section an American coal ball, from which has come this valuable contribution to paleobotanical knowledge.

The Pennsylvanian period contains all the known coal beds of Illinois, lying unconformably upon the Mississippian, and covered with unconsolidated material, either glacial drift or alluvium. The Illinois Pennsylvanian is divided into three formations. In ascending order these are the Pottsville, the Carbondale, and the McLeansboro. The base of coal seam no. 2 is arbitrarily taken as the upper limit of the Pottsville formation, and the top of coal seam no. 6 as the upper limit of the Carbondale formation. Coal

seam no. 5, then, falls within the upper portion of the Carbondale formation. Fig. 1 is a columnar section taken in the region of the O'Gara mine no. 9, from which the coal ball was taken, and shows the position of seam no. 5 in relation to seams no. 2 and no. 6, and to the Illinois formations of the Pennsylvanian period.

Based on a study of the fossil flora of the coal beds and associated strata by WHITE (9), the Carbondale formation of Illinois may roughly be correlated with the Allegheny of the Appalachian coal region. Similarly, the Illinois Pottsville corresponds in a general way to the Pottsville of Pennsylvania and the McLeansboro to the Conemaugh. Additional evidence of the geological age of the stem in question is found in a study of other plant structures contained

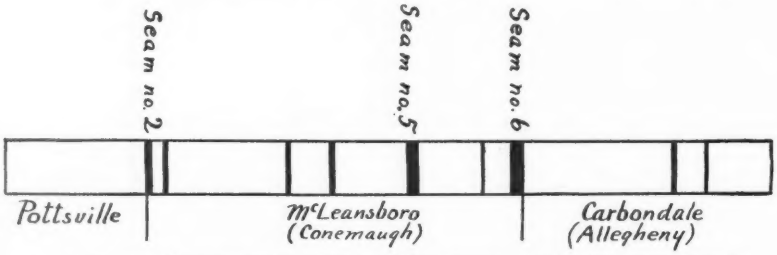

FIG. 1.—Columnar section taken in Saline County, Illinois, showing position of coal seam no. 5 in relation to Illinois formations of Pennsylvanian period.

within the coal ball from which the sections were made. Of these associated structures, those which have been identified, and which will be described in a later paper, belong to what is considered a typical Carboniferous flora; that is, Lepidodendroid material which is not known to exist in the Mesozoic, and cross-sections of certain fern petioles, heretofore known only from the Carboniferous of England. Furthermore, no coal balls, of which this concretion definitely was an example, are known to occur elsewhere than in the coal seams of the Paleozoic.

The portion of the stem preserved was approximately 4 cm. long and 2 cm. in diameter. Rootlets have penetrated the stem, which is very slightly compressed, so that a complete cross-section was not obtained. The actual diameter, therefore, might have been slightly larger. Pyrite is present in the sections in small

quantities, insufficient to hinder observation. Preservation of the tissues is good, showing the details of the phloem in a few instances, although in most bundles the phloem is entirely gone.

The diagram of the cross-section (fig. 2) shows the essential features. Placed near the periphery are numerous groups of small hexagonal and thick-walled sclerenchymatous cells, arranged in four or five irregular concentric rows. One of these groups is shown in fig. 3. The cross-section of the stem is solid, the large parenchyma-

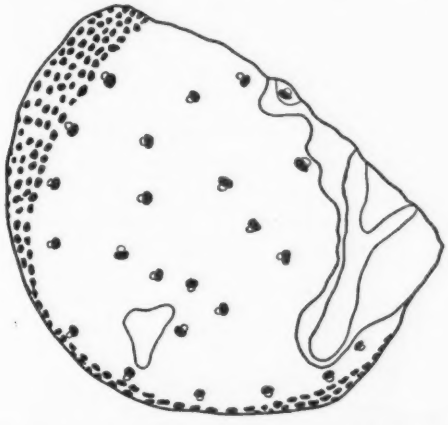

FIG. 2.—Diagram of cross-section of stem with peripheral groups of sclerenchymatous cells and scattered collateral bundles; xylem shown in black; rootlet has penetrated one side of stem.

tous cells, roughly hexagonal, differing only in the thicker walls of those nearer the periphery, as may be seen in a comparison of the parenchyma cells in fig. 3 with those adjacent to a vascular bundle from a more central portion of the stem (fig. 5). Throughout the cross-section are scattered what probably were mucilage ducts (fig. 4). These ducts, usually surrounded by smaller cells, are considerably elongated in longitudinal section (fig. 6).

Scattered throughout the cross-section are numerous endarch collateral closed bundles. With slight variation the phloem is always orientated toward the periphery (fig. 2). The details of a single bundle with phloem preserved are shown in fig. 5. Partially

surrounding the xylem is a sheath of small heavy-walled sclerenchyma fibers, from one to three cells in width. This sheath never extends completely around the bundle, nor is it present on the

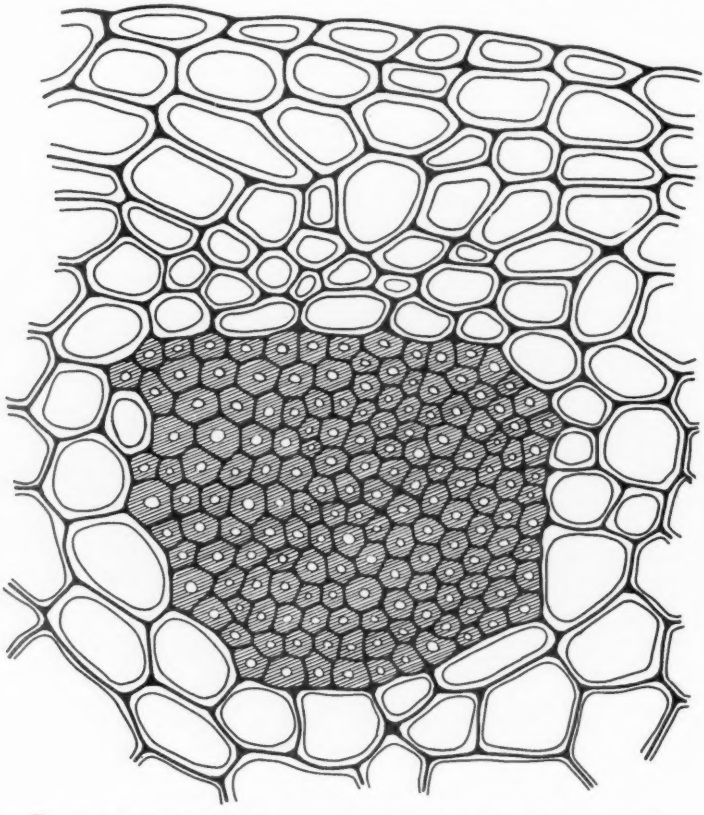

FIG. 3.—Cross-section of one of numerous groups of heavy-walled sclerenchyma cells surrounded by parenchyma; ×110.

phloem side. Between this sheath and the heavy-walled xylem cells are usually present thin-walled parenchyma, frequently appearing very like a pericycle, although in no case was it possible to trace these cells around the phloem.

The vessels are much elongated and of the spiral type exclusively, pitted vessels being entirely absent. In connection with these vessels there is strong evidence in favor of the monocotyledonous position of the stem. The tracheids of gymnosperms, with the exception of the Gnetales, have tapering ends. The vessels of pteridophytes as well as those of Gnetales and the perennial dicotyledons have inclined cross walls, in some cases at a large angle. In the case of monocotyledons, however, and the extremely herbaceous dicotyledons, according to JEFFREY (5) the terminal walls of

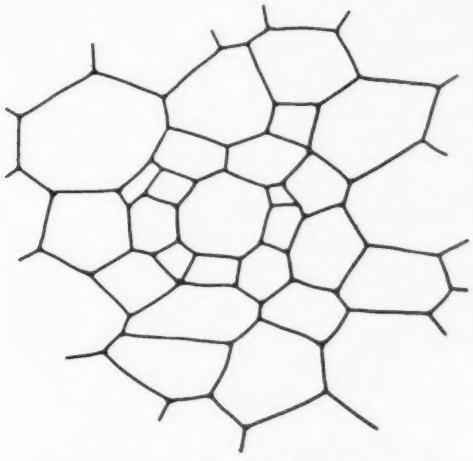

FIG. 4.—Cross-section of mucilage duct; ×70.

the vessels are practically horizontal. Fig. 7 shows a longitudinal view of a vessel from this fossil stem, in which the end wall is practically at right angles.

The phloem was not preserved in most cases. In the bundle shown in fig. 5, in which the phloem has not been lost, it may seem to consist entirely of thin-walled cells arranged in such a way as to suggest most forcibly that it consists entirely of sieve tubes and their companion cells. Unfortunately, no sieve plates were found nor could definite phloem tissue be distinguished in longitudinal view.

A consideration of these facts warrants the conclusion that the fossil stem in question should be placed in the monocotyledon branch of the angiosperms, and that its geological horizon is the American Carboniferous. This description differs in all fundamental respects from that of any known cycadean petiole type such as *Mylloxylon*

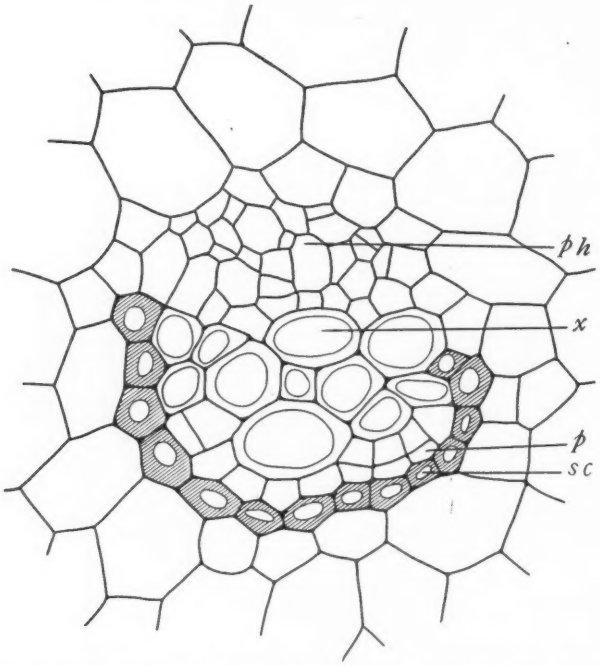

FIG. 5.—Cross-section of vascular bundle: *sc*, sheath; *x*, xylem; *ph*, phloem; *p*, parenchyma; ×350.

(7). Although a comparative study with living monocotyledons has brought out some favorable comparisons, there is at hand insufficient information of this sort to make a more definite statement as to its phylogenetic position, which it is hoped further work will make possible. For this first Paleozoic angiosperm to be described, the following name is therefore proposed:

Angiospermophyton americanum, gen. et sp. nov.

Questions involving the origin of angiosperms or the relative antiquity of monocotyledons and dicotyledons are not necessarily affected by this discovery, except in the one important connection that this single example of an angiospermic flora in the Paleozoic is sufficient to throw light on the problems arising from the so-called

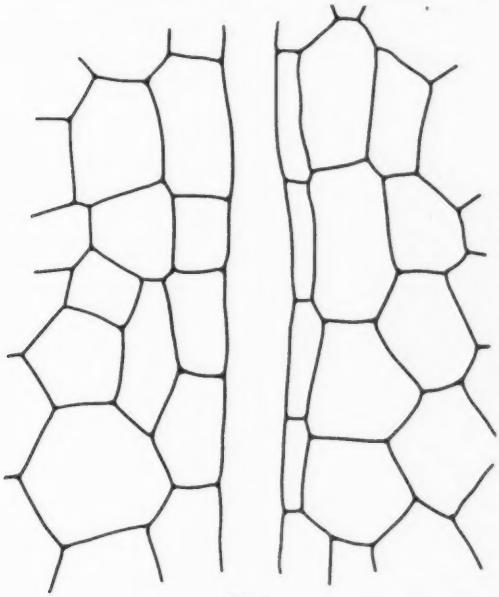

FIG. 6

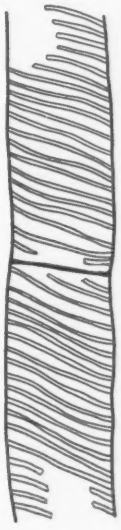

FIG. 7

FIGS. 6, 7.—Fig. 6, longitudinal section of mucilage duct; ×140; fig. 7, longitudinal view of spiral vessel, showing nearly horizontal end wall; ×200.

sudden appearance of the large and modern angiosperm flora in the Cretaceous, by pointing out that the place of attack on the origin of angiosperms must be Carboniferous or pre-Carboniferous. Why angiosperms have not been found in abundance before the Cretaceous is a question which is more puzzling because of definite knowledge of their earlier appearance. It may be related, as BERRY is quoted by GUPPY (3), to a long antecedent evolution in "areas

remote from regions of sedimentation," or it may be due to the fact that only a limited portion of the existing plant deposits of the world as yet has been carefully investigated.

Summary

1. American coal balls showing preserved plant structure have been sectioned.

2. From an Illinois coal ball from the Carbondale formation were obtained sections of a monocotyledonous stem, with collateral closed bundles scattered throughout the solid cross-section.

3. The vessels were of the spiral type exclusively, with transverse end walls. The phloem consisted of sieve tubes and what appeared to be companion cells.

4. Around the periphery of the stem, arranged in four or five irregular concentric rows, were groups of hexagonal, small, heavy-walled sclerenchyma cells.

5. This is the first angiosperm described from the Paleozoic, and the name *Angiospermophyton americanum* is proposed.

6. No attempt is made as yet to correlate this with any living group.

7. This announcement throws no light on the phylogenetic origin of the angiosperms, but does remove the problem from the Mesozoic to the Carboniferous or pre-Carboniferous.

This paper has been made possible through the generosity of Dr. A. C. Noé, who has turned over to me these first American coal balls for sectioning, and who has been a constant source of information and inspiration during the preparation of material and manuscript. I also wish to express my appreciation to Dr. W. J. G. Land for instruction in the preparation of rock sections and for numerous critical observations and suggestions as to interpretation of structures.

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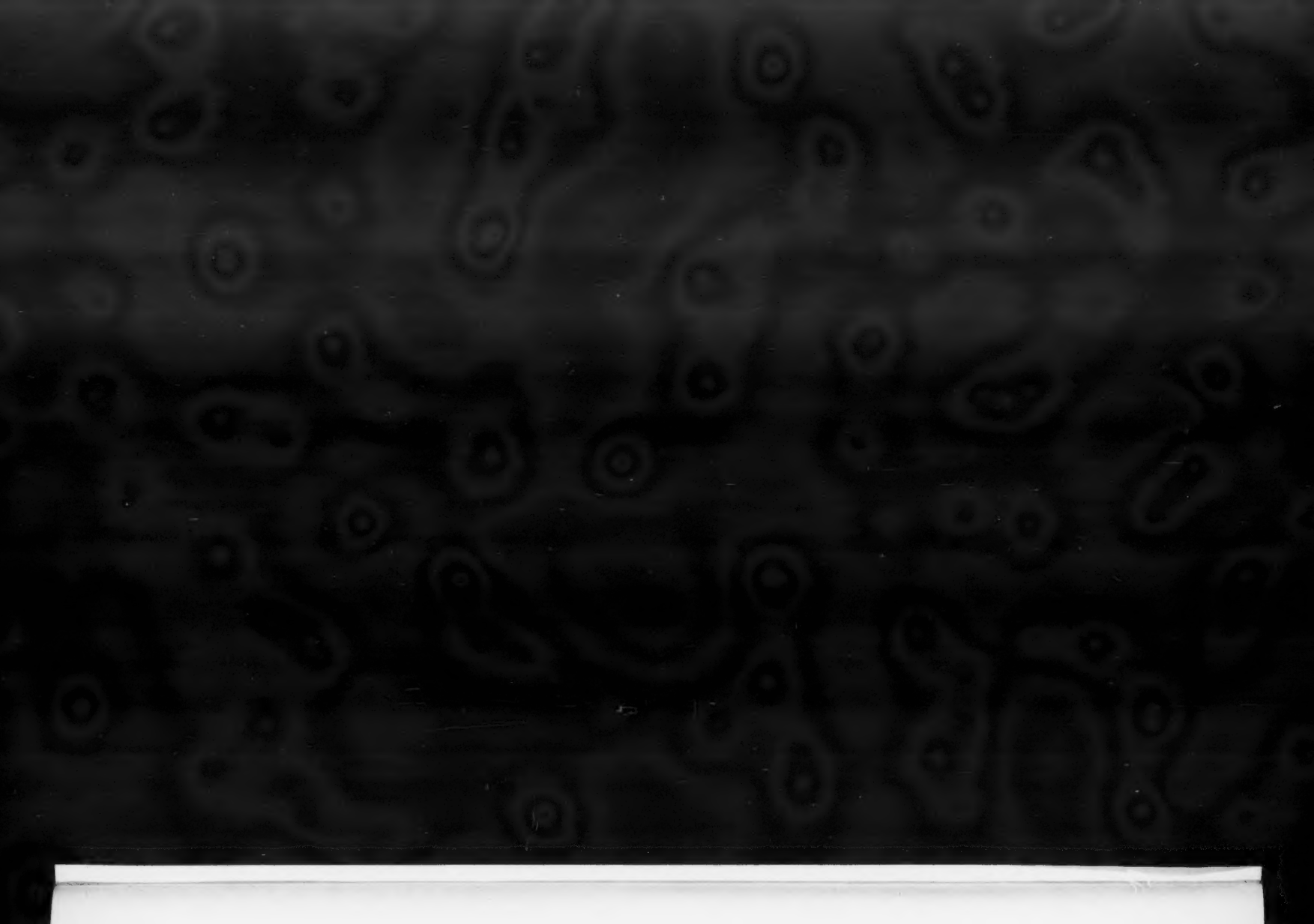

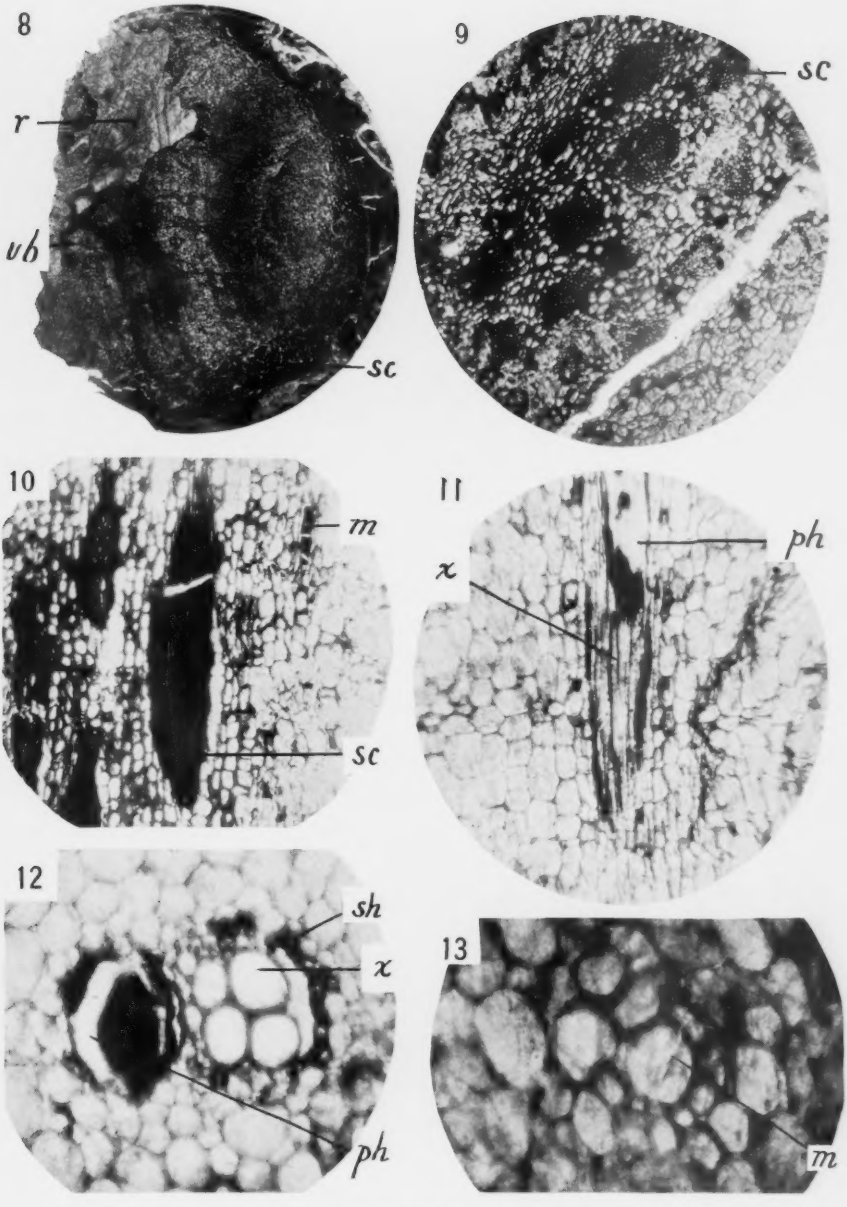

HOSKINS on PALEOZOIC ANGIOSPERM

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EXPLANATION OF PLATE XVII

Photomicrographs by Lillian G. Reynolds.

FIG. 8.—Cross-section of *Angiospermophyton americanum: sc*, group of sclerenchyma cells of peripheral region; *vb*, vascular bundle; *r*, lepidodendroid rootlet; ×3.

FIG. 9.—Cross-section of outer portion of stem; *sc*, group of sclerenchyma cells; ×25.

FIG. 10.—Longitudinal section of outer portion of stem; *sc*, sclerenchyma; *m*, mucilage duct; ×25.

FIG. 11.—Longitudinal view of vascular bundle; *x*, spiral vessels; *ph*, region of phloem; ×35.

FIG. 12.—Cross-section of vascular bundle; *sh*, sheath; *x*, xylem; *ph*, region of phloem (in this instance almost entirely gone); ×85.

FIG. 13.—Cross-section of mucilage duct (*m*); ×35.

SEASONAL VARIATION OF SULPHUR CONTENT IN CERTAIN TISSUES OF THE APPLE TREE[1]

R. S. MARSH

(WITH NINE FIGURES)

Introduction

Sulphur is an element essential to plant life. It has been found to be indispensable in the formation of all plant proteins. Because of an intimate connection between protein compounds and life processes, they probably have physiological functions in the formation of other compounds. Sulphur has also been found in compounds of plant tissue other than the protein groups. Although an essential element, sulphur has not received the attention given other important mineral elements. This fact is probably due to the old method of analysis showing very small amounts of sulphur in plant tissues, the comparatively large amounts found in certain soils, the replenishing of sulphur to the soil by rainfall, and to certain undesirable effects produced by liberal applications of sulphur to the soil. Recent work, however, has tended to modify the earlier views on this subject.

Since the advent of the Osborne or sodium peroxide method for the determination of sulphur in organic materials, there have been many interesting data published showing the amounts of this element in certain plant tissues. AMES and BOLTZ (2) made the following summary and comparison from observed data: the percentage of sulphur often exceeds that of phosphorus in leguminous plants, it equals one-half that of phosphorus in cereal plants, and the amount of sulphur in cruciferous plants is always greater than that of phosphorus. The amount of sulphur in plant tissue not only varies with the kind of plant but may vary according to the amount available in the soil. This is well brought out by the data in Table I, after SWANSON and MILLER (14).

On both clover and oats the effect of the treatment on the analysis is very marked. Moreover, the increased yields of the

[1] Contribution from the Horticultural Department of the University of Missouri.

two crops seemed to depend more on sulphur than on any other ingredient. AMES and BOLTZ obtained similar results with potassium sulphate applied to tobacco plants in the field. HAYWOOD (6), BUCKHOUT (3), and WIDTSOE (15) found that sulphur was taken into plant tissues in such large amounts as to cause injury. Their data were obtained in vicinities of smelters, where abnormal amounts of sulphur gases were liberated and added to the soil by rainfall. DEMOLON (4) noticed that sulphur had a very marked effect on the development of chlorophyll. The leaves of the plants on the sulphur plots were a darker green than those on the untreated plots. Later DULEY (5) noticed that atomic sulphur in a nutrient

TABLE I

EFFECT OF FERTILIZERS ON YIELD AND CHEMICAL CONTENT OF OATS AND CLOVER

OATS				CLOVER			
Weight	Percentage sulphur	Percentage nitrogen	Treatment	Weight	Percentage sulphur	Percentage nitrogen	Treatment
2.01	0.175	0.32	$CaSO_4+NaNO_3$	3.98	0.197	2.94	$CaSO_4+NaNO_3$
2.01	0.113	0.33	$Na_2SO_4+NaNO_3$	4.06	0.181	2.93	$Na_2SO_4+NaNO_3$
1.75	0.30	0.21	$S+NaNO_3+CaCO_3$	3.89	0.198	3.10	$S+NaNO_3+CaCO_3$
1.68	0.005	0.54	$NaNO_3$	1.76	0.097	2.32	$NaNO_3$

solution seemed to increase the chlorophyll content in leaves of the corn plant.

NICHOLAS (11) observed that 200 kg. of sulphur per hectare (178 pounds per acre) on beans gave a maximum starch accumulation, while 300 kg. of sulphur per hectare (267 pounds per acre) gave the greatest starch content in peas. The photosynthetic processes were found to be stimulated by the proper amounts of sulphur added to the soil. MONTEMARTINI (10) found that there are several essential mineral elements that pass from the leaves to the stems at night, but that sulphur and silicon are exceptions. RIPPEL (13) found that sulphur was not mobilized in the spurs, and that there was no migration of sulphur from regions of storage to new tissues in the spring. He inferred from this that there was no withdrawal of sulphur from leaves to the branches in the fall.

He also made analyses of twigs of *Salix fragilis* collected in the spring, and found the sulphur content to be 0.1014 per cent, while the phosphorus content varied between 0.078 and 0.15 per cent. He noted that phosphorus was mobilized but that sulphur was not.

In brief, our present knowledge of sulphur may be summarized as follows. The sulphur content of plant tissue is greater than previously assumed, often being as high or even higher than the phosphorus content. The natural sulphur supply in the soil may be exhausted by cultivation, leaching, and plant absorption. Sufficient amounts are not supplied through rainfall completely to counteract the removal through drainage and plant intake. Phosphorus, nitric nitrogen, and potassium are often made more available through the use of fertilizers containing sulphates and flowers of sulphur. Sulphur fertilization increases the sulphur content of plants, and in many instances increases the yield. Sulphur fertilization often increases the plant's intake of other mineral elements, and aids in the greater development of chlorophyll. Chlorosis and a decrease of starch content will result from the lack of sulphur.

This study was undertaken to determine the amount of sulphur in different tissues of the apple tree at various seasons of the year. The experiment supplements the chemical data on the apple spur as published in Missouri Station Research Bulletin 40.

Materials and method

Samples for analysis were collected from mature Wealthy and Payne Late Keeper apple trees, standing in adjacent rows. They were in excellent condition, although the orchard had been in sod for some years. Wealthy is an alternate bearer at Columbia, while Payne Late Keeper is an annual bearer, spur records showing that it may bear fruit on the same spurs two or three years in succession. Samples of leaves, spurs, young and old bark were collected during the forenoon after two days of clear weather. The leaves were counted, the old bark was taken from trunks and limbs more than 3 inches in diameter, and the young bark from branches 0.75–1.25 inches in diameter. Samples were taken in 1921 on May 7, May 13, May 17, July 31, September 17, and November 5, and in 1922 on January 22 and March 18. Samples

of spurs were also taken from Ben Davis, Gano, Jonathan, and York Imperial May 11 and July 3, 1922. Bearing spurs were used from the first three varieties, while non-bearing spurs were collected from the York Imperial trees. Where sulphur-containing spray solutions had been applied to the trees, the samples were thoroughly washed and care was taken to check the analyses with those of unsprayed trees. In most instances spray mixtures were not applied to the trees that were sampled. Immediately after collection in the orchard, the samples were weighed and placed in a constant temperature oven, where they remained until dried to constant weight, and were then pulverized in a mill. Two gram samples were used for the sulphur determinations.

METHOD OF ANALYSIS.—After trying some of the better methods of sulphur analysis, the one given by the Association of Official Agricultural Chemists was finally adopted, with certain modifications suggested by DR. C. R. MOULTON of the Department of Agricultural Chemistry of the University of Missouri. The method is given in detail.

Ten grams of sulphur-free sodium peroxide was placed in a 250 cc. nickel crucible, and just enough water added to bring the reaction to completion. The crucible was then heated over an alcohol lamp until all the water was expelled. After cooling, 2 gm. of the organic material was rapidly added and thoroughly mixed. The crucible and contents were then heated slowly from thirty to forty minutes, until frothing had ceased and the mass had subsided. At this time the contents will have a black oily appearance on top. Sodium peroxide in small amounts was added until sparks and flashes failed to appear, and then the heating was continued for five minutes at a red heat. When crucible and contents had cooled, they were added to a beaker which contained 200 cc. of water, and the crucible was carefully washed. This solution was acidified with hydrochloric acid and boiled until all the excess HCl was driven off. After this solution had been exactly neutralized with NH_4OH, it was diluted to a 400 cc. volume, and 4 cc. of HCl added. A 10 per cent barium chloride solution was added to the solution while boiling. The solution was then placed in a hot oven (75°–80° C.), left for twelve hours, and then removed, filtered, and washed with

hot water containing a trace of HCl. A final washing was given with pure water until the precipitate was freed from all chlorides. The precipitate was then dried, ignited, and weighed. This weight was divided by two and multiplied by the factor 0.13738, which gave the amount of sulphur as S. The percentages of dry weight are given in fig. 1 and table II.

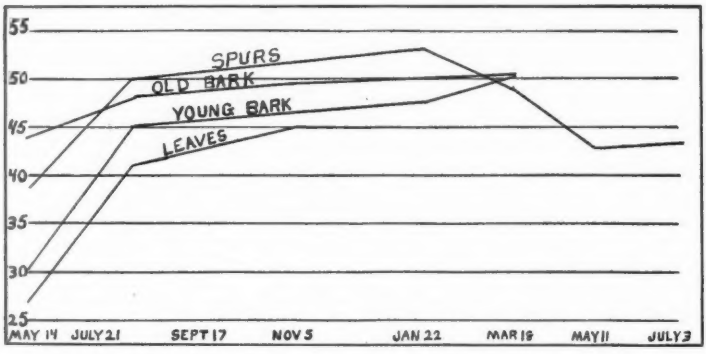

FIG. 1.—Percentages of dry weight in spurs, leaves, old and young bark at different seasons of year.

TABLE II

DRY WEIGHT, IN PERCENTAGES OF FRESH WEIGHT

Date	Leaves	Spurs	Young bark	Old bark
May 14, 1921	27	39	30	44
July 21, 1921	41.5	50	45	47.8
November 5, 1921	45	52	50	49.5
January 22, 1922	.....	53	47.3	50
March 18, 1922	.....	48.6	50.9	50.5
May 11, 1922	.....	44.1	.....	.....
July 3, 1922	.....	45	.....	.....

As shown by fig. 1, there is a general increase in dry weight from May until January, except in the case of the spurs. The percentage of dry weight remained rather constant from January until March, showing a slight increase in young bark and a similar decrease in spurs. The bearing spurs have a larger percentage of dry weight in May and a smaller percentage in July, as compared with the non-bearing spurs of the previous year.

The sulphur determinations are given for the leaf samples in percentages of dry weight in fig. 2 and table III. In May, leaves of bearing spurs of Wealthy contained 0.265 per cent, and those of

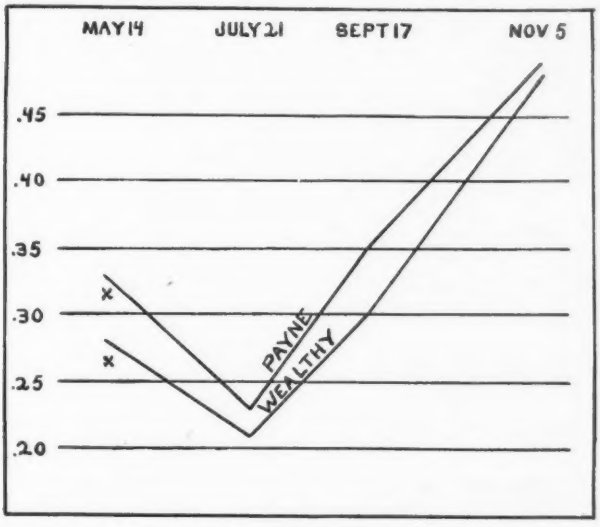

FIG. 2.—Variation in percentages of sulphur in leaves throughout year, leaves from non-bearing spurs; *x*, percentages of sulphur in leaves from bearing spurs.

TABLE III

SULPHUR IN PER CENTAGES OF DRY WEIGHT IN APPLE LEAVES, ALSO GRAMS OF SULPHUR PER LEAF

DATE	PERCENTAGE OF DRY WEIGHT		GRAMS PER LEAF	
	Wealthy	Payne Late Keeper	Wealthy	Payne Late Keeper
May 14, 1921.....	0.283	0.331	0.000092556	0.00016721
July 21, 1921.....	0.21	0.23	0.0002364	0.0002071
September 17, 1921.....	0.30	0.33	.....	.....
November 5, 1921.....	0.485	0.489	0.00058945	0.000370028

Payne Late Keeper 0.31 per cent sulphur, both approximately 0.02 per cent less than the non-bearing spurs. The curves for these two apple varieties in fig. 2 show that the sulphur content of Payne

Late Keeper is always greater than that for Wealthy. The least difference occurs in November and the greatest in September. The minimum is reached in May by both varieties, and from May until November there is a rapid but steady increase. In November the sulphur content had increased 121 per cent over that of May.

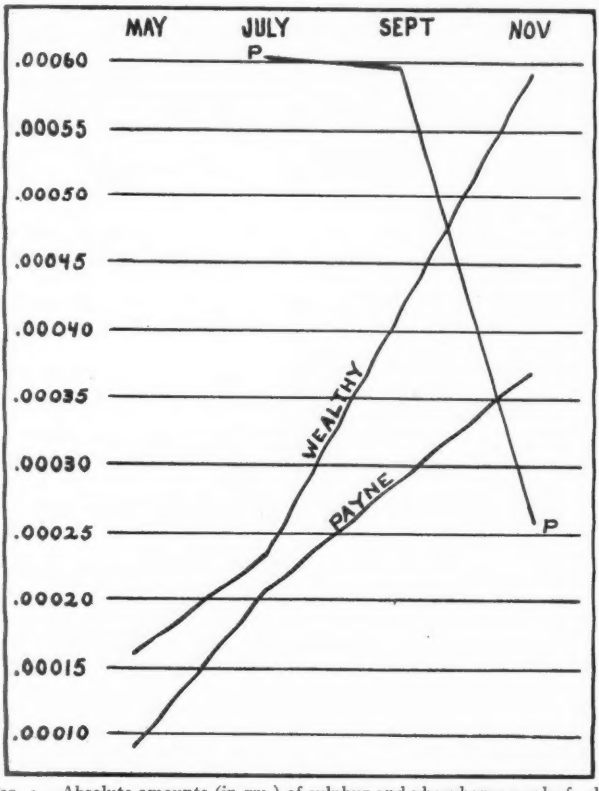

FIG. 3.—Absolute amounts (in gm.) of sulphur and phosphorus per leaf; data for phosphorus curve (*PP*) taken from RICHTER.

The absolute amounts of sulphur in the leaves of various ages are shown in table III and fig. 3. The curves in fig. 3 show graphically that the Wealthy leaves have higher absolute amounts throughout the season. The curves also show the absence of a July minimum, which characterized the sulphur percentage curves

for leaves on a dry weight basis. This difference is due to an increased size of leaves. Payne Late Keeper has a higher percentage content of sulphur, but because of the smaller size of its leaves it does not have as much sulphur per leaf as the Wealthy.

The sulphur determinations as obtained in the analysis of young bark are given in table IV and fig. 4. The curves in fig. 4 show a

TABLE IV

SULPHUR IN YOUNG AND OLD BARK OF APPLE IN PERCENTAGES OF DRY WEIGHT

DATE	YOUNG BARK		OLD BARK	
	Wealthy	Payne Late Keeper	Wealthy	Payne Late Keeper
May 14, 1921	0.2080	0.1717	0.080	0.1000
July 21, 1921	0.1003	0.0870	0.087	0.1043
September 17, 1921	0.1079	0.1003	0.0998	0.1097
November 5, 1921	0.1003	0.0970	0.1003	0.1126
January 22, 1922	0.2074	0.1598	0.0790	0.0865
March 18, 1922	0.1510	0.1390	0.0970	0.1003

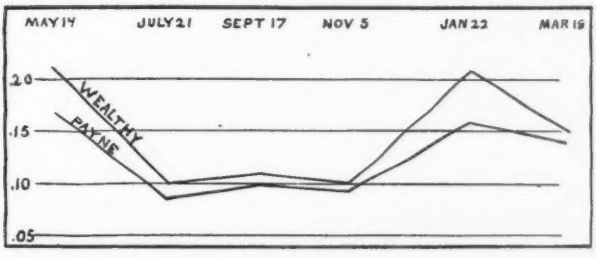

FIG. 4.—Variation in percentages of sulphur in young bark during different seasons of year.

decided downward trend from May until July; from July to November there is but slight variation. A rise in the percentages of sulphur is found between November and January, which almost equals the fall between May and July. The curve is characterized by two maxima and two minima. In every instance the sulphur content of Wealthy slightly exceeds that of Payne Late Keeper. The greatest difference between the two occurs in January. The young bark averages twice as much sulphur in May and January

as in July, September, and November. The sulphur percentages in old bark are given in table IV and fig. 5. The graph in fig. 5

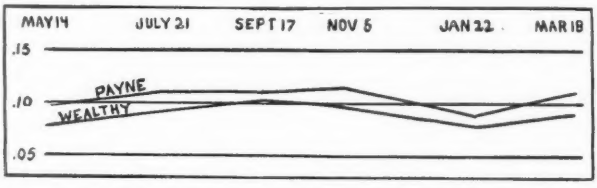

FIG. 5.—Variation in percentages of sulphur in old bark during different seasons of year.

shows that the old bark presents the least seasonal variation in sulphur content. The maximum is reached in November and the minimum in January, but the difference between these two points is only 0.02–0.026 per cent. The Payne Late Keeper is consistently higher in sulphur percentages than the Wealthy, but both have similar seasonal variations, and the difference between the two is always small.

The values for the sulphur content of apple spurs are given in percentages of dry weight in table V and fig. 6. The curves

TABLE V

SULPHUR IN SPURS OF APPLE IN PERCENTAGES OF DRY WEIGHT

DATE	NON-BEARING SPURS		BEARING SPURS			
	Wealthy	Payne Late Keeper	York	Ben Davis	Jonathan	Gano
May 14, 1921	0.200	0.18	.....	.....	.....	.....
July 31, 1921	0.144	0.129	.....	.....	.....	.....
September 17, 1921	0.25	0.20	.....	.....	.....	.....
November 5, 1921	0.236	0.126	.....	.....	.....	.....
January 22, 1922	0.143	0.121	.....	.....	.....	.....
March 18, 1922	0.180	0.166	.....	.....	.....	.....
May 11, 1922	.....	.....	0.23	0.119	0.153	0.137
July 3, 1922	.....	.....	0.17	0.09	0.098	0.107

showing the percentages of sulphur in spurs are characterized by two minima which occur in July and January. The direction of variation of all varieties is the same, but a considerable difference occurs in November between Wealthy and Payne Late Keeper, and between the bearing and non-bearing spurs in May and July.

The sulphur content in the non-bearing Payne Late Keeper is always less than the non-bearing spurs of Wealthy or York. Of the bearing

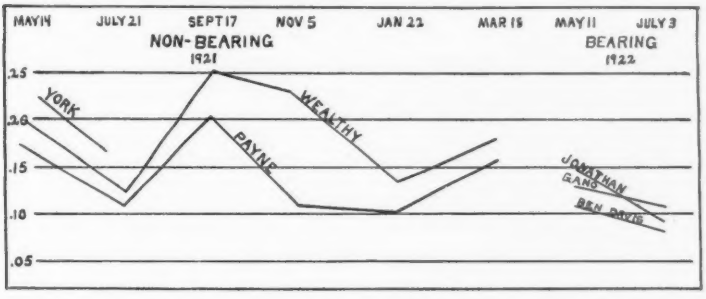

FIG. 6.—Variation in percentages of sulphur in spurs during different seasons.

spurs the Ben Davis is consistently less than the other two bearing varieties, Jonathan and Gano, for 1922.

Discussion

The amount of sulphur contained in the apple tree tissues studied is of the same order as phosphorus. At certain seasons of the year the percentage sulphur content may exceed the phosphorus; at others the percentage phosphorus content will be greater. This is especially true in the leaves, spurs, and young bark, as shown in figs. 3, 7, 8.

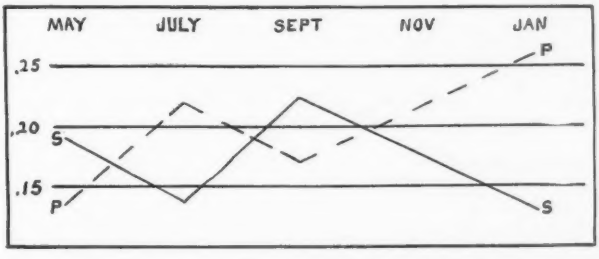

FIG. 7.—Percentages of sulphur and phosphorus in spurs at different seasons of year; phosphorus data for curve (*PP*) taken from HOOKER (1920).

The greatest amount of sulphur (0.22–0.48 per cent) is found in the leaves; apple spurs have the next highest content (0.09–0.25

per cent); and third in order is young bark, varying between 0.10 and 0.20 per cent. Old bark has the least amount among the tissues investigated, the percentages ranging between 0.08 and 0.10 per cent.

In comparing the sulphur and phosphorus content, there is found to be an inverse relationship in leaves, old bark, and spurs (figs. 3, 7, 8). In every instance where there is an increase in the percentage of sulphur, there is a corresponding decrease in the phosphorus percentage, and vice versa. The sums of the phosphorus and sulphur percentages give a constant value of approximately 0.39 per cent in non-bearing spurs during September, November,

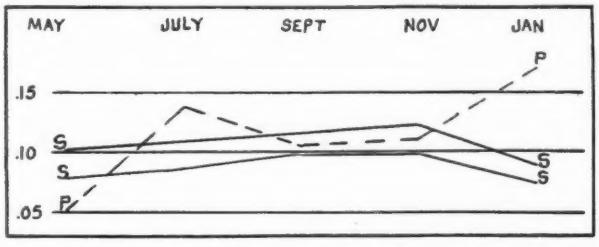

FIG. 8.—Seasonal variation in percentages of sulphur and phosphorus in old bark; data for phosphorus curve (*PP*) taken from HOOKER (1922).

and January. The phosphorus content in bearing spurs does not have this inverse relationship with sulphur.

Another interesting correlation exists between the trend of sulphur percentage and the H-ion concentration. ABBOTT (1) presents data which show the same trend of H-ion concentration as of the sulphur percentage for non-bearing spurs. This comparison is given in fig. 9. MITRA'S (9) H-ion concentration curve also parallels the sulphur percentage curve. March data seem to be the only exception found in this parallelism, as taken from the ABBOTT data. It seems logical to associate this with the greater dissociation of H-ions in sulphuric acid, although the presence of other acids must not be ignored.

The evidence greatly favors the view that sulphur is not mobilized to the extent that phosphorus and potassium are. Experimental data show that the greatest amounts of sulphur occur in

the leaves just before they fall. In this respect sulphur is similar to calcium. The sulphur is not drawn back from the leaves to regions of storage. RIPPEL (13) predicted a similar conclusion from observations made on *Salix fragilis*. Since the phosphorus and sulphur percentage curves have an inverse relationship, the possibility is suggested that one of the factors involved in the mobilization of phosphorus is its replacement and liberation by sulphur. The minimum sulphur content is reached in July in the

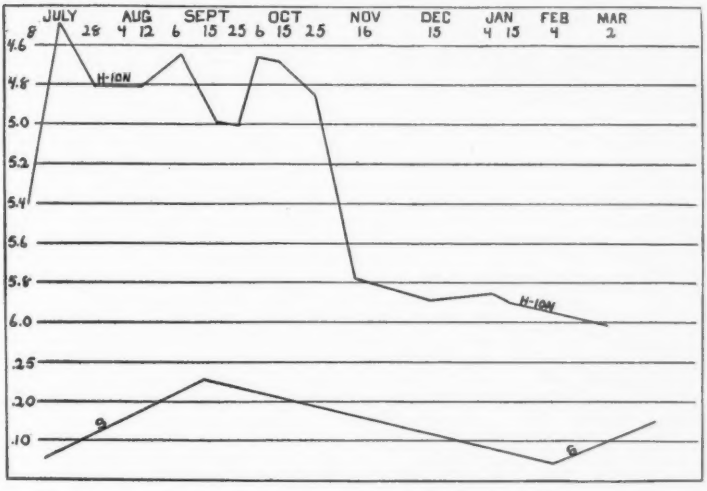

FIG. 9.—Comparison of sulphur content of non-bearing apple spurs with their H-ion concentration at different seasons; H-ion data taken from ABBOTT.

young bark, leaves, and spur tissues. There is an increase in September.

There is nothing in the experimental work here reported to indicate that under ordinary conditions bearing apple trees are unable to secure sulphur from the soil in amounts sufficient to meet all requirements. The fact that considerable quantities are lost (or eliminated) at the time of leaf abscission even suggests that possibly more is absorbed than is required. On the other hand, the distinct seasonal changes found in the sulphur content of certain tissues, particularly the bark and spurs, suggest that sulphur-

containing compounds may be important, either directly or indirectly, in determining the exact character of the seasonal life history of the tree. It is not without interest that a rise in sulphur content in the spurs comes at a time when they are entering their rest period, and that apparently fruit-bud differentiation in spurs takes place only during that period while their sulphur content is low. Particularly interesting is the inverse relationship found between sulphur and phosphorus content. The full significance of these relationships cannot be stated at the present stage of this investigation. It suggests, however, that the intake, translocation, synthesis, and utilization of phosphorus and sulphur are only different aspects of the same nutritional problem.

Summary

1. The sulphur content, as determined by the sodium peroxide method, is of the same order as the phosphorus content in the apple tree tissues investigated.

2. The highest percentages of sulphur are found in the leaves, and then in descending order in spurs, young bark, and old bark.

3. The sulphur content varies inversely with the phosphorus content throughout the year.

4. Sulphur resembles calcium in that it is not mobilized to any great extent.

5. The seasonal variation of sulphur is parallel with the H-ion concentration.

6. The percentage of sulphur is at a minimum in the apple spur at the time of fruit-bud differentiation.

I am indebted to Dr. H. D. HOOKER, JR., for suggestions, constructive criticisms, and some of the references to the literature.

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COLUMBIA, MO.

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REVEGETATION OF A DENUDED AREA. II

HENRY S. CONARD

(WITH TWO FIGURES)

In July, 1911, I examined and described[1] the beginnings of vegetation on a gravel area that had just been laid bare along the Long Island Railroad west of Cold Spring Harbor station. Owing to difficulty in obtaining right of way east of this point, the projected railroad was not built, and this area has been left almost untouched by man since that time. It is greatly regretted that no botanist has surveyed it in the intervening years. The present paper reports conditions found in July, 1922.

The area now has a thicket of *Robinia Pseudo-Acacia* and other saplings, 10–15 feet high, along the middle, broken by low areas of *Myrica asplenifolia*, herbs, and bare gravel. Near the present railroad bank the vegetation is sparse and low. At the foot of the bluff there are bare places, thickets of *M. Gale*, etc., or beds of herbaceous plants. *Smilax glauca* climbs over the shrubbery everywhere. The steeply cut slopes from the natural hilltop to the plain are only partly stabilized; much gravel still slides down in places. The low bank shown in fig. 1 of the former report (fig. 1) is now covered with *Andropogon scoparius* and *Lysimachia quadrifolia*, completely stabilized. The higher slopes are dotted with stumps and sods from the overhanging hill tops, together with some newly established herbaceous or even woody seedlings (*Hieracium paniculatum*, *Solidago bicolor*, *Juniperus virginiana*, *Myrica Gale*). At the extreme west end of the area, the bank is stabilized and held in place by a complete covering of grasses and other perennial herbs and small shrubs. Large areas of the flat, especially at the middle and western parts, are covered almost exclusively by *Rubus villosus*. A large gravelly area (200 feet long) at the west end is covered with *Hypericum gentianoides*, edged with an area of *Deschampsia*. Near the east end, a large

[1] CONARD, H. S., Revegetation of a denuded area. BOT. GAZ. 55:80–84. 1913.

flat is covered chiefly by *Andropogon scoparius*. The abundance of other species is indicated by the following lists, listed in each case with the most abundant first.

Woody plants.—Robinia Pseudo-Acacia, Myrica asplenifolia, Rubus allegheniensis, R. villosus, Myrica Gale, Gaylussacia baccata, Betula populifolia, Smilax glauca, Rhus glabra, R. Toxicodendron, Vaccinium vacillans, Sassafras

FIG. 1.—Foot of slope (right) and part of level area (left); from same point as fig. 1 of former report.

variifolium, Prunus serotina, Quercus marilandica, Q. alba, Rhus copallina, Castanea dentata.

Herbaceous plants occurring in dense beds.—Andropogon scoparius, Hypericum gentianoides, Lespedeza hirta, Pteris aquilina, Desmodium marilandicum, Lysimachia quadrifolia, Potentilla canadensis, Lespedeza capitata, Deschampsia flexuosa, Tephrosia virginiana, Crotalaria sagittalis, Gnaphalium polycephalum, Desmodium rotundifolium.

Herbs scattered about generally.—Rumex acetosella, Eupatorium hyssopifolium, Aster linariifolius, Baptisia tinctoria, Solidago bicolor, S. juncea, S. nemoralis, Helianthemum canadense, H. majus, Lechea intermedia, Linaria canadensis, Muhlenbergia capillaris, Trichostema dichotoma, Lactuca canadensis, Lespedeza virginica, L. frutescens, L. repens, Sericocarpus asteroides.

The soil apparently remains unchanged except on the actual surface. Under the larger shrubs and saplings there is an accumula-

FIG. 2.—Bluff shown in fig. 2 of former report.

tion of dead leaves, largely undecayed, which are slowly giving a humus content, or at least a humus covering, to the ground. Colonies of small ants appear to be the only agency that can mix this humus with the gravel and sand. A fertile soil must await the action of earth-worms and insects, or the accumulation of dead roots.

In the former survey, 60 species of Angiosperms and one fern were found on the denuded area. Of these 61 species, 53 were native to the hillside above the cut, 39 of the 53 being long-lived perennials. Now 121 species are listed. Fifteen species present

in 1911 are now absent. Of these, the following are common weeds of cultivated, that is, fertile soil.

Acalypha virginica, Avena sativa, Oxalis corniculata, Plantago major, Portulaca oleracea, Polygonum hydropiper, Taraxacum officinale, Xanthium canadense.

The absence of these may be attributed to the following causes. The raw glacial sand and gravel, devoid of humus, is not suitable for an ordinary ruderal succession, such as occurs on fertile, well tilled ground, and many well adapted native plants were present in the ground as left by the graders. *Aralia nudicaulis*, *Aster* sp., *Desmodium nudiflorum*, *D. canescens*, *Stylosanthes biflora*, *Thaspium aureum*, and *Smilax rotundifolia* have found the conditions of the flat too severe for permanent survival. They lived for a time because they were transplanted bodily. *Ambrosia artemisiaefolia*, *Oenothera biennis*, and *Polygonum convolvulus*, present in 1911, persist on the new ground, without invading the hillside above the cut. *Achillea millefolium*, *Carya alba*, *Cyperus filiculmis*, *Euphorbia ippecacuanhae*, *Lespedeza repens*, *Solidago rugosa*, *S. tenuifolia*, and *Stenophyllus capillaris* are found both on the hill and on the new ground, as in 1911. *Carya* and *Smilacina* have not perceptibly increased in number.

Seventy-five additional species have appeared on the denuded area. Of these, 14 were observed in 1911 on the hillside that was partly dug away to make the new exposure. Twenty-five biennials and perennials were found this year on the hillside, all of which must have been present or nearby in 1911, although not noted in the previous paper. Of these, 17 have settled already on the new ground. From the age of some of the tree sprouts, it is probable that they spring from transplants that had not shown themselves in 1911. Other saplings were certainly seedlings. Thus 31 new immigrants from the hillside now appear below, making (with 46 spp. persisting since 1911) a total of 77 species of the adjacent native plants that are re-established. The remaining 44 species newly appearing on the denuded area are immigrants from greater distances. Of these, 31 are natives and 13 introduced (indicated by *x*), mostly from Europe, that is, weeds and forage grasses.

New plants on the denuded area in 1922.

From the hillside.—Acer rubrum, Amelanchier canadensis, Antennaria neglecta, Betula populifolia, Chrysopsis mariana, Danthonia spicata, Desmodium canadense, D. marilandicum, Gaylussacia baccata, Helianthemum majus, Hieracium scabrum, H. venosum, H. Gronovii, Hypericum gentianoides, Lechea intermedia, L. minor, Lespedeza hirta, Lysimachia quadrifolia, Panicum dichotomum, Potentilla canadensis, Psedera quinquefolia, Populus grandidentata, Quercus coccinea, Q. rubra, Q. stellata, Q. velutina, Rubus allegheniensis, Solidago caesia, Verbascum Thapsus, Viola ovata.

From elsewhere (not found on hill).—Agrostis alba *x*, A. hyemalis, Angelica villosa, Asclepias incarnata, A. syriaca, Aster ericiodes, Bidens frondosa, Carex cephaloidea (?), Cassia nictitans, Chrysanthemum Leucanthemum *x*, Crotalaria sagittalis, Daucus Carota *x*, Digitaria sanguinalis *x*, Diodia teres, Eragrostis pectinacea, Erigeron annuus, E. canadensis, Gnaphalium polycephalum, Juniperus virginiana, Hieracium paniculatum, Hypericum perforatum *x*, Lactuca canadensis, Lepidium virginicum, Lespedeza capitata, Linaria vulgaris *x*, Panicum clandestinum, P. microcarpon, Phleum pratense *x*, Plantago lanceolata *x*, Poa compressa *x*, Polygonum pennsylvanicum, Pyrus arbutifolia, P. communis *x*, P. malus *x*, Rhus Toxicodendron, Salix alba *x*, Salix tristis (?), Sisyrinchium atlanticum, Solidago canadensis, S. nemoralis, S. juncea ramosa, Muhlenbergia capillaris, Tridens flavus, Trifolium repens *x*.

Comparing this list with the list of most abundant plants, it is notable that the most abundant plants are all natives excepting *Rumex acetosella*, in spite of the fact that many introduced weeds are scattered about the area.

Incidentally, the changes in the flora of the undisturbed hillside are instructive. Fifteen species have appeared over and above those long-lived perennials now detected for the first time. These are believed to be newcomers.

Anaphalis margaritacea, Angelica villosa, Desmodium canadense, Galium circaezans, Hypericum punctatum, Lactuca canadensis, Solidago graminifolia, Strophostyles helvola, Tridens flavus, Viola ovata, Hieracium paniculatum, Solidago juncea ramosa, Bidens frondosa, Gnaphalium polycephalum.

Eighteen species found on the hillside in 1911 have now disappeared, as follows.

Desmodium sp., Eupatorium hyssopifolium, Mollugo verticillata, Myrica Gale, Phytolacca decandra, Plantago major, Portulaca oleracea, Stylosanthes biflora, Taraxacum officinale, Thaspium aureum, Viola pedata, Xanthium canadense, Carex sp., Lupinus perennis, Gerardia flava, Antennaria neglecta, Erechtites hieracifolia, Oxalis corniculata.

Thus we find, along with a stable and permanent group of annuals, biennials, and perennials, another group which are migratory, appearing now here, now there. We have to do here mostly with weeds, those vegetable tramps. Do these migratory plants render the soil unfavorable for their subsequent growth, as is said to be the case with wheat? The whole problem of "auto-intoxication" of soil by plants, poisonous excretions, etc., might well be investigated by a comparative study of the effects upon soil of plants which do and do not appear continually in the same place.

The hillside plants that have never appeared on the new ground form an interesting list of 24 species.

Aster divaricatus, A. undulatus, Carex sp., Chimaphila maculata, Corylus americana, Cunila mariana, Cypripedium acaule, Epigaea repens, Gerardia flava, G. pedicularia, Galium circaezans, Erechtites hieracifolia, Hypericum punctatum, Hypoxis hirsuta, Linum virginianum, Lupinus perennis, Nyssa sylvatica, Oakesia sessilifolia, Panicum sp., Pedicularis canadensis, Quercus ilicifolia, Q. Prinos, Solidago graminifolia, Strophostyles helvola.

Chimaphila, *Cypripedium*, *Epigaea*, and the two species of *Gerardia* are known to have peculiar soil requirements. The first two are mycorrhiza plants, and the species of *Gerardia* are root parasites. Probably *Epigaea* is a mycorrhiza plant. *Pedicularis* may be a mycorrhiza plant or a root parasite. *Nyssa sylvatica* is distinctly out of place on this gravelly hill. It belongs in low, moist soil. The trees here are too small to bear flowers or seeds. The failure of the other species to move down is not so easily explained.

Mosses abound in some places, but they have not hitherto played any important rôle in the taming of this new naked gravel. On the contrary, we have a succession clearly led off and dominated by the native vascular plants. The first were those that survived the steam shovel, being mostly transplanted bodily. Another army of indigens came in by wind, gravity, birds, and other animals. By wind, birds, and other animals a number of weeds have entered. There is a row of gardens 200 feet south of and below this plot, across the railroad tracks, and the weeds appear mostly on the edge of gravel nearest these gardens. Among these weeds there has been

a high mortality, and they are still in strictly subordinate positions. Such ubiquitous weeds as *Chenopodium album*, *Taraxacum*, *Amaranthus* spp., and *Galinsoga* are wholly absent.[1] By the time the soil is rich enough to enable the weeds to take possession, the natives will already be too strongly entrenched to be disturbed by them. We have, therefore, a succession of a totally different type from that shown in the reversion of fertile soils to a wild state. The condition of neighboring gravel slides and beaches along the shore of Long Island Sound bears out this conclusion. These naturally denuded areas show various stages of a very slow succession of native plants.

In this inland, artificial, level gravel area, the succession is proceeding rapidly enough to be readily observed. Another ten years should give the transition from shrub and scrub to forest. Thus we may see in facts of recorded change on one area that which we can only infer from a comparative study of many other areas in various stages of the same or a similar succession.

BROOKLYN ACADEMY OF ARTS AND SCIENCES
COLD SPRING HARBOR, LONG ISLAND, N.Y.

[1] *Centaurea nigra* and *Paspalum setaceum* occur just west of the area, on the same flat railroad bed.

A SUSPENSOR IN ANGIOPTERIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 306

W. J. G. LAND

(WITH TWO FIGURES)

The suspensor in plants is a structure which appears in early embryonal life, and serves to bring the embryo into more favorable food relations than it at first enjoyed. A suspensor may be developed in any plant phylum having either a massive or a compact gametophyte, and may be long retained by those phyla whose gametophytes are verging toward extinction. The suspensor appears rarely in Bryophytes, here and there in Pteridophytes, reaches a climax in Gymnosperms, declines and is sometimes absent in Angiosperms. In Pteridophytes a suspensor is common in Lycopodiales, and among Filicales in Ophioglossaceae and Marattiaceae. In the latter family CAMPBELL[1] reports a suspensor in *Danaea*, the occidental member; the present account adds *Angiopteris*, the most widely distributed oriental and austral member.

The writer was fortunate in finding, on the island of Tutuila, quite a number of adult plants of *Angiopteris evecta* Hoffm., and many hundreds of gametophytes in various stages of development. This island, 14° 18′ S, 170° 42′ W, gives a most favorable view of vegetation under a continuous optimum condition of growth. The temperature throughout the year has a daily range of 26°–34° C. approximately, the minimum being shortly after midnight, the maximum in midafternoon. The altitude (650 m.) is high enough and the island small enough to have abundant and almost uniform daily precipitation on all sides, which, subject as it is to the trade winds, would not be the case were it larger and much higher, or were the altitude only slightly above sea level. The atmosphere is always near the saturation point, and the rainfall is

[1] CAMPBELL, D. H., The Eusporangiatae. The comparative morphology of the Ophioglossaceae and Marattiaceae. Washington. 1911.

sometimes excessive, a fall of 38 cm. in five hours having been reported. The slopes are very steep, giving perfect drainage, their surfaces covered with densely matted vegetation which prevents excessive evaporation. There are very few breaks in the forest roof.

The adult sporophyte individuals of *Angiopteris evecta*, relatively few in number, are more numerous on the unstable banks of the channels cut by water rushing down the very steep mountain sides. Their altitude range is from a few meters above tide water to 100 m. Individuals were noted with trunks 100 cm. high, 70 cm. in diameter, with leaves 5–6 m. long and every pinna crowded with sporangia. It was estimated that the crown of one of these large plants had a potential output of over two billions of spores. Of this enormous output, not one may produce a plant able to live beyond the sporeling stage.

Gametophytes were found only on bare friable soil, usually back in pockets in the eroding banks in light so dim that the smaller ones were visible with difficulty. Photographically the light was approximately 1/3000 that of the open. The friable soil was continually falling and burying the prothallia, some of which, although completely buried, were still vigorous and bore sporelings. This condition is very suggestive of the way in which the subterranean habit of the gametophytes of some Lycopodiaceae and the Ophioglossaceae may have originated. Perhaps the thallus of *Angiopteris* is well on the way toward the subterranean habit. It is quite thick, and in many individuals the ventral sex organ pad has become a more or less massive cylindrical structure. In some this cylindrical development has been carried so far that the wings of the thallus are inconspicuous, and some of the sex organs are lateral and dorsal. Hence we have morphologically dorsal antheridia and physiologically dorsal antheridia and archegonia separated from each other by the lateral wings of the thallus. It should be noted that only those archegonia which are ventral have been observed to function. The thallus has also definitely acquired an endophytic intracellular fungus, evidently related to those found in Lycopodiaceae and Ophioglossaceae. The hyphae, as well as the antheridia and oogonia, are large and clear and can be studied with little difficulty.

The massive archegonial pad bears numerous archegonia, but never more than one has been observed to function. Several thousand individuals were examined, and never more than one embryo or sporeling was found on a prothallus. It is very evident that the failure of all eggs but one to function is not due

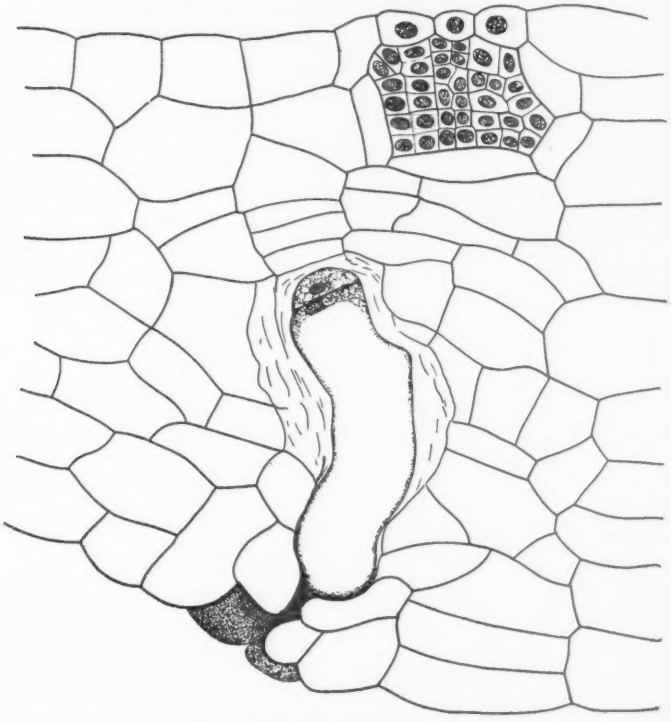

FIG. 1.—Embryo of two cells, showing proximal cell thrusting distal cell deeper into thallus; ×400.

to absence of sperms, since numerous antheridia are present on both the dorsal and ventral surfaces. The necks of the functionless archegonia fail to open. In no instance was an opening through the outer tier of neck cells found in functionless archegonia. The outer tier of four cells remains firmly united long after the contents of the archegonium have broken down. Finally the neck cells break

away from the thallus as a united mass. The neck cells are very different from the other cells of the thallus, in that they are densely packed with cytoplasm and food materials, the older ones showing no vacuolation even when examined with objectives of 1.40 aperture under critical lighting.

The functioning egg elongates along the major axis of the archegonium and divides transversely, the proximal cell producing the suspensor, the distal cell producing the embryo proper. The suspensor cell elongates and thrusts the embryonal cell deeply into the storage region of the relatively massive gametophyte (fig. 1).

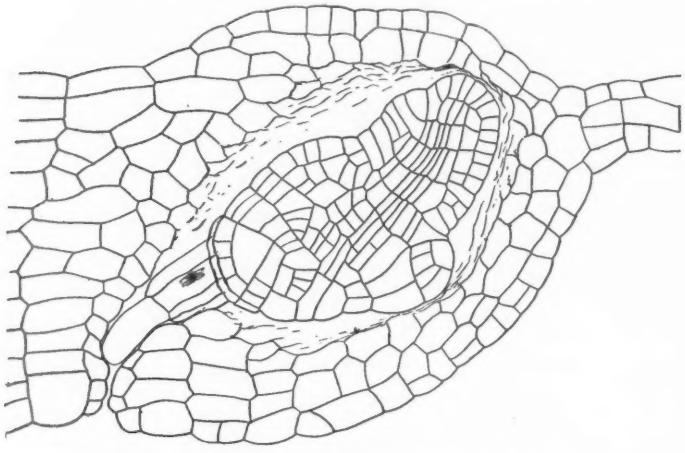

FIG. 2.—Embryo with suspensor of several cells; ×120.

Longitudinal and transverse divisions follow (fig. 2), giving rise to a more or less massive suspensor. Also the first cells of the root cap may slightly elongate and give rise to a structure comparable with the secondary suspensor of Gymnosperms. No trace of a suspensor could be found in some embryos, and it is believed that the suspensor is not constant in *Angiopteris*.

When the suspensor first appears (Bryophytes) it is derived from the distal cell, thrusts deeply into the adjacent storage regions, takes up food and passes it on to the embryonal cells, and continues active until the peripheral cells of the foot begin to function actively

as haustoria. Thus throughout its existence it functions solely as a haustorium and never acquires a new function. In Pteridophytes, Gymnosperms, and Angiosperms it is derived from the proximal cell or cells, and in consequence thrusts the embryonal cells bodily into the adjacent storage region, and when at its best (Gymnosperms) by its constant thrust keeps the embryo in sharp contact with the most abundant source of food. Later, as it declines (Angiosperms), it again becomes truly haustorial. It is evident that when it first appears in plants it has a single rôle, that of a true haustorium; when at its best a dual rôle, first, a true haustorium, second, mechanical thrust. As it declines the last acquired function is lost and it again becomes solely haustorial.

In the two great antithetic plant phyla, the Bryophyte line and the Pteridophyte-Gymnosperm-Angiosperm line, the suspensor rises in a radically different way. In Bryophytes, the line of gametophyte dominance and sporophyte extinction, it rises from the distal region of the embryo; in the Pteridophyte-Spermatophyte line, the line of sporophyte dominance and gametophyte extinction, it rises from the proximal region of the embryo.

A suspensor may be expected in any plant phylum having either a compact or a massive gametophyte. When present in thallose gametophytes it is at the beginning of its career; when present in the feeble gametophytes of Angiosperms it seems to be well on the way toward extinction.

The determining factor in suspensor formation seems to be the relation of the functioning egg to the food supply. When the food supply is concentric to the egg no suspensor will be formed; when excentric a suspensor will be formed, the size of the suspensor varying with the volume of the excentric food mass.

UNIVERSITY OF CHICAGO

CURRENT LITERATURE

BOOK REVIEWS

The maize plant

It has often been urged that the specialization of the last few decades has not only stolen much of the charm from the study of botany, but has also made it difficult for the student to get a true, properly proportioned picture of the living plant as a whole, playing its rôle in nature and in civilization. No book could be much more successful in escaping this criticism than the present volume by WEATHERWAX.[1] The subject matter, treating of the maize plant not only from man's utilitarian point of view, but also depicting its characteristics as a "biological individuality," is both scientifically handled and put into a very readable form.

Following a brief introduction, the author commences with a chapter (II) on "Names and relationships." Here he emphasizes that the only serviceable taxonomic name is the generalized *Zea Mays* L.; "references to variations and to agricultural varieties may better be made by structural and physiological terminology than by Linnaean binomials." Chapter III is on "History and geographical distribution." It seems clearly established that the birthplace of maize is Central America, from which source it may have been introduced into China before 1492. In chapter IV, in considering the "Botanical origin" of maize, the author refutes the idea that it is a descendant from teosinte, or from a cross between teosinte and some wild prototype of maize. He believes that *Zea, Euchlaena,* and *Tripsacum* have descended directly and independently from a common ancestor (probably a herbaceous perennial) now extinct.

Chapters V–IX deal with "Structure and germination of the seed," "Anatomy and physiology of the stem," "Structure and functions of the leaf," "Branches of the shoot," and "The root system," the descriptions being condensed and specific for the corn plant. In chapter X, the subject of "Ecological relations" is qualified as follows: "Modern maize is so far removed from the conditions that surrounded its wild ancestor that little is known of its natural environment in early times; and its ecology is reduced to a problem not of the plant but of man who acts as its agent." A brief treatment of insect and fungous diseases is included. Chapters XI–XIII take up the practical matters of "Seed and planting, Tillage, and Harvesting."

[1] WEATHERWAX, PAUL, The story of the maize plant, pp. xvi+247. *pls.* 2 (colored). *figs.* 174. Univ. Chicago Press. 1923. $1.75.

In Chapters XIV and XV, "The inflorescence" and "Spikelets and flowers," the author presents a thorough but concise description of the normal morphology, and also describes and discusses many interesting anatomical and sexual anomalies in the reproductive parts. It is suggested that maize may be on the way toward dioecism, or at least dimorphism, with one form monoecious and the other staminate. Several theories on the origin of the ear are discussed, but none is regarded as satisfactory. Chapters XVI and XVII provide complete, authoritative accounts of "Pollination," and "Gametogenesis and fecundation." In Chapter XVIII, "The fruit," the range of variation in the ear is outlined and the basis for judging "show corn" summarized. Two short chapters (XIX XX), on "The embryo" and "The seed coat" are concise morphological descriptions, evidently based on the author's own investigation.

In an interesting chapter (XXI) on "The endosperm," the author presents the cytology of endosperm development, the storage of protein and carbohydrate in endosperms of different varieties, and a brief discussion of "popability." It is pointed out that in the endosperm cells there is usually much variation from the expected triploid number of chromosomes, through imperfect mitotic divisions and the frequent occurrence of "direct" divisions. EMERSON's[2] explanation of endosperm mosaics on this basis (non-disjunction) is recognized, but not regarded as "thoroughly satisfactory." Chapter XXII, "Physical character of the caryopsis," discusses variation in size and shape of grains.

In chapter XXIII, on "Heredity," attention is given only to some of the situations that are rather peculiar to corn, that is, certain endosperm characters. A brief account is given of the facts and common theories of hybrid vigor; the author feels that this phenomenon has not yet been completely explained. This is followed by two practical chapters (XXIV, XXV) on "Breeding," and "Products and uses;" and the text is closed with two historical chapters (XXVI, XXVII) on "Maize in aboriginal America," and "Maize in American life."

Throughout there is an admirable conciseness of presentation. The book is well illustrated, and contains a bibliography of 172 titles.—M. C. COULTER.

Outline of Genetics

The *Outline of genetics, with special reference to plant material* by MERLE C. COULTER[3] is a thorough revision of *Plant genetics* by JOHN M. COULTER and MERLE C. COULTER, published five years ago. Much new material has been added, so as to include the essential features of the recent developments in genetics. The book is designed to meet the needs of students in other lines of investigation who may wish to have the more important facts and theories in

[2] BOT. GAZ. **73**:158. 1922.

[3] COULTER, MERLE C., Outline of genetics, with special reference to plant material. pp. 211. *figs.* 31. Univ. Chicago Press. 1923.

genetics available in as brief a form as possible. It is admirably suited for this purpose. The more technical parts are indicated by smaller type, so that the reader need not go at all extensively into the subject and can still get a comprehensive view of the fast widening field of genetics. The reader with no biological training will also be able to use the book to advantage, although some subjects are discussed too briefly and too technically to be entirely clear. Animal illustrations are used wherever necessary to bring out important similarities and differences in inheritance in the two classes of organisms.

The student of genetics will find the chapters in the gametophyte and the endosperm in inheritance, and sex-determination in plants particularly valuable. The very brief treatment of the gametophyte might well include the observation of BELLING[4] on the abortion of half the pollen grains in the tetrads of *Rhododendron*, and the demonstration by PARNELL[5] of chemical differences in the pollen grains formed by a segregating rice plant. It is interesting to note that the latter condition has also been found by DEMEREC in the pollen of a waxy-starchy corn hybrid.

The distinction between "determiner" and "factor" is somewhat forced. The determiner is considered as a unit which brings about a visible effect independently of other units of inheritance, whereas a factor must work in conjunction with other units to make a visible effect. If this distinction is made, units which are considered as determiners when first discovered may later have to be classed as factors when other complementary units are discovered. It is impossible to conceive of a unit in inheritance not being dependent upon something else for its visible expression.

A notable feature is the impartial attitude taken toward all disputed interpretations. All sides are given fairly and the reader is left to draw his own conclusions. The same clear, concise, and readable style which characterized the former book has been used throughout. This little volume can be recommended without reservation for crowded bookshelves, as the amount of information it gives is unusually large in comparison with the space it occupies.—D. F. JONES.

MINOR NOTICES

Palladin's Plant physiology.—The second American edition of PALLADIN'S[6] *Plant physiology* has been prepared by LIVINGSTON. The changes in the text are very slight, involving a few corrections of the earlier edition and the addition of a few references. The main change has been the addition of a brief summary of each chapter at its close. These summaries will be helpful to the student in

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[4] Ann. Report Department Genetics, Carnegie Inst. Washington. 1921 (pp. 110 and 111).

[5] Jour. Genetics **11**: 209–212. 1921.

[6] PALLADIN, V. I., Plant physiology, translated by B. E. LIVINGSTON. 8vo. pp. xxxiii+360. Philadelphia: P. Blakiston's Son and Co. 1923.

grasping the main points. A portrait of PALLADIN appears as a frontispiece, with an accompanying note of appreciation of his contributions to plant physiology, and a brief sketch of his life. The text is commendable particularly for the numerous citations of literature, and for its treatment of the subject of respiration in plants.—C. A. SHULL.

Theoretical and applied colloid chemistry.—The second American edition of OSTWALD's lectures, translated from the eighth German edition by FISCHER,[7] appears without radical changes from the first edition. Some sections have been slightly enlarged, as for instance the section on the colloid chemistry of foods. One new figure is added. The book is one of the most readable introductions to the colloidal state that beginners could find.—C. A. SHULL.

NOTES FOR STUDENTS

Taxonomic notes.—BRITTON[8], in continuing his studies of West Indian plants, has published 69 new species, representing 50 genera, most of them from Cuba.

PAYSON[9] has studied *Thelypodium* and certain allied genera (*Warea*, *Stanleyella*, *Chlorocrambe*, *Caulanthus*, and *Streptanthella*), not only from the taxonomic point of view, but also from the standpoint of phylogeny.

DE CANDOLLE[10] has published new species of Piperaceae from the following localities: Formosa (5 spp.), Brazil (4 spp.), Colombia and Peru (25 spp.), Ecuador (25 spp.), Java (11 spp.), Borneo and Sumatra (26 spp.), Celebes (12 spp.), Mexico (21 spp.), a total of 129 new species in *Piper* and *Peperomia*.

EVANS[11] has published a very full account of the Chilean species of *Metzgeria*. The species of this genus "form a conspicuous part of the hepatic flora of Chile and the neighboring antarctic regions of South America." He recognizes eleven species, two of which are new.

GAUMANN[12] has described the species of *Peronospora* upon Euphorbiaceae (5 spp., 3 new) and Polygonaceae (4 spp., 1 new).

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[7] OSTWALD, WOLFGANG, Theoretical and applied colloid chemistry, translated by FISCHER, M. H. pp. 12+266. John Wiley and Sons. 1922.

[8] BRITTON, N. L., Studies of West Indian plants. XI. Bull. Torr. Bot. Club **50**:35–56. 1923.

[9] PAYSON, E. B., A monographic study of *Thelypodium* and its immediate allies. Ann. Mo. Bot. Gard. **9**:233–324. 1922.

[10] DE CANDOLLE, CASIMIR, Piperaceae. Ann. Conserv. Jard. Bot. Genève **21**:221–322. 1920.

[11] EVANS, A. W., The Chilean species of *Metzgeria*. Proc. Amer. Acad. **58**:271–324. *figs. 10*. 1923.

[12] GAUMANN, ERNEST, Les espèces de *Peronospora* sur les Euphorbiacées et les Polygonacées. Ann. Conserv. Jard. Bot. Genève **21**:1–23. *figs. 7*. 1919.

HASSLER, E.,[13] has presented several families as represented in Paraguay, with the following results: Lauraceae, 28 spp., 6 new; Myrsinaceae, 11 spp., 1 new; Moraceae, 20 spp., 4 new; Urticaceae, 12 spp.

MARIE-VICTORIN[14] has published an account of the ferns of the province of Quebec. The taxonomic presentation is preceded by a description of the ecological conditions involved. The 62 distinct species described include a number of ecological varieties. The species are grouped as 32 mesophytes, 21 xerophytes, and 9 hydrophytes.—J. M. C.

Revegetation of tussock grassland.—In the montane regions of South Island, New Zealand, under a climate of considerable aridity, due to low rainfall (at times as little as 14 inches of annual precipitation), high winds, and high summer temperature, the natural vegetation of tussock grasses and shrubs has been completely destroyed. According to COCKAYNE[15] this has been accomplished by over grazing and by burning over the tussock grassland in order to produce fresh succulent new growth for the sheep. An entirely new vegetation of very different character has replaced the tussocks, and the pasture value of the mountain slope has been much reduced. This new vegetation is very sparse, consisting largely of small cushions of various species of *Raoulia*, a few small grasses, and many introduced weedy plants, the general aspect being decidedly that of a desert. Curiously enough the plants most productive of forage in the depleted pastures are the introduced and weedy *Rumex acetosella* and *Erodium cicutarium*. The sparsity of the plant cover under the new conditions exposes the fertile soil to the destructive action of both wind and water erosion, making very difficult conditions for the establishment of seedlings, a difficulty accentuated by the introduction of rabbits that have become very numerous and very destructive to yŏung plants. COCKAYNE emphasizes the importance of bringing ecological science to assist in the solution of these problems, and gives the results of excluding sheep and rabbits from selected areas and of seeding in different ways with various mixtures of the seeds of grasses and other plants. The examination of the conditions, the planning of the experiments, and the analysis of the results all go to show the ability of the ecologist to contribute to the solution of many of the practical problems of plant production.—GEO. D. FULLER.

Feeding power of plants.—The ability of plants to secure and utilize essential elements from relatively insoluble materials is sometimes spoken of as

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[13] HASSLER, E., Lauracearum Paraguariensium conspectus. Ann. Conserv. Jard. Bot. Genève **21**:73–97. 1919; Myrsinacearum, *idem* 99–107; Moracearum, *idem* 109–131; Urticacearum, *idem* 141–216.

[14] MARIE-VICTORIN, FR., Les Filicinées du Quebec. Contrib. Lab. Bot. Univ. Montreal. no. 2. pp. 98. 1923.

[15] COCKAYNE, L., An economic investigation of the montane tussock grassland of New Zealand. XII. The regrassing experiments in Central Otago. New Zealand Jour. Agric. **24**:321–334. *figs. 6.* 1922; **25**:1–11, 129–144. *figs. 8.* 1922.

feeding power. TRUOG[16] places much importance upon the general law of chemical equilibrium and the acidity of plant juices as determining the feeding power of plants. The law of chemical equilibrium operates at two points, in the soil about the absorbing roots, and within the plant where the inorganic plant food materials are being precipitated from the cell sap. When two soluble products are formed by the action of carbonated water on a mineral in the region of the absorbing roots, the foraging capacity is considered dependent upon the removal of both soluble products, either by the plant or otherwise. When only one soluble product is formed, the feeding power is believed to depend upon the acidity of the plant sap, and the consequent ease or difficulty of precipitation from the sap solution. If the basic ions are utilized for the regulation of sap acidity, the more acid the sap the greater is the feeding power. On the other hand, if the basic substances go to the formation of protein complexes, metal proteinates, the more acid the sap the less is the feeding power, due to the difficulty of precipitating metallic ions from more acid solutions. Other factors may be involved, but TRUOG believes these to be the controlling influences in general. Numerous examples are cited to illustrate the general principles. In a more recent paper, DAVIS, HOAGLAND, and LIPMAN[17] offer trenchant criticisms of TRUOG's theory.—R. B. DUSTMAN.

Forest trees of Hokkaido, Japan.—MIYABE[18] and his colleagues have continued their work on what promises to be a monumental publication on the trees of Japan. The artistic and typographical features of the earlier parts, as already noted in this journal,[19] seem to have been fully maintained. The present fascicles consist of colored plates of the foliage, flowers, fruit, buds, seeds, and seedling stages of various Japanese trees, with descriptive text in both Japanese and English. One plate by CHUSUKE SUZAKI is devoted to each of the following species: *Populus Maximowiczii*, *P. Sieboldi*, *Salix urbaniana*, *S. jessoensis*, *S. caprea*, *S. rorida*. *S. viminalis* var. *yezoensis*, *S. sachalinensis*, *S. Miyabeana*, *Juglans Sieboldiana*, *Pterocarya rhoifolia*, *Carpinus cordata*, *C. laxiflora*, *Ostrya japonica*, *Betula Miximowicziana*, *B. Ermanii*, *B. japonica*, and *Alnus japonica*.—GEO. D. FULLER.

Vegetation of Greenland.—This report by HOLTTUM[20] is the first attempt to apply the principles of succession to the vegetation of the west shore of Green-

[16] TRUOG, E., The feeding power of plants. Science **56**:294–298. 1922.

[17] DAVIS, A. R., HOAGLAND, D. R., and LIPMAN, C. B., The feeding power of plants. Science **57**:299–301. 1923.

[18] MIYABE, KINGO, and KUDO, YUSHUN, Icones of the essential forest trees of Hokkaido. Pub. by Hokkaido government. Sapporo. 10.5×15 in. fasc. **4**:39–47. *pls. 11–13.* 1921; fasc. **5**:48–56. *pls. 14–16.* 1921; fasc. **6**:57–64. *pls. 17–19.* 1921; fasc. **7**:65–74. *pls. 20–22.* 1922; fasc. **8**:75–85. *pls. 23–25.* 1922; fasc. **9**:86–98. *pls. 26–28.* 1923.

[19] BOT. GAZ. **72**:55. 1921.

[20] HOLTTUM, R. E., The vegetation of west Greenland. Jour. Ecol. **10**:87–108. *pls. 3.* 1922.

land. The oceanic climate with its cool damp summer causes the vegetation of long stretches of the coast to be very uniform in character. Two regions are distinguished, separated by the parallel of 62° N. latitude and by the July isotherm of 10° C. The northern division has for its climax a heath dominated by *Empetrum nigrum* and *Cassiope tetragona*, with species of *Vaccinium*, *Ledum*, and *Rhododendron* locally abundant. In the xerarch succession lichens and mosses are conspicuous, while in the lower stages of the hydrarch series *Hippuris* and *Menyanthes* are most abundant. The southern region culminates in a scrub forest of *Betula odorata*, with which are associated such shrubs as *Alnus ovata*, *Sorbus americana*, and *Salix glauca*. There are interesting notes on the successions and the growth forms. Anthocyan pigments and mycorhizal fungi seem to be particularly abundant.—GEO. D. FULLER.

Migration of African flora.—Southeast Africa possesses a flora composed of a tropical or subtropical element, and a temperate or mountain element. The trees and shrubs of the forest, according to BEWS[21], are found to tend to migrate along the main river valleys at right angles to the coast. The migration of the tropical flora and the derived subtropical species has been largely along the coastal belt. Floral morphology shows that the subtropical is largely a derivative from the older tropical, and that such specialized forms as those possessing succulence and spinescence have developed in response to the drier subtropical conditions. The mountain ranges parallel to the coast form a great line of migration for the temperate element. Tropical growth forms seem the more primitive, that is, they are largely uniform, woody, and mesophytic; while temperate forms are more diverse, including herbaceous, bulbous, and tuberous plants with divided leaves that appear to be largely derivative.—GEO. D. FULLER.

Photoperception.—The supporters of the rival intensity and direction theories of photoperception seem unable to convince one another and reach definite conclusions as to the cause of light response in plants. LUNDEGARDH,[22] working on coleoptiles of *Avena*, directed the light rays so as to strike the tip of the coleoptile tangentially, from a direction perpendicular to the axis of the coleoptile; also from above, so as to illuminate just one-half of the tip. Taking into consideration the fact that tangentially striking rays are refracted a certain amount when they enter the coleoptile, his results lead him to conclude that the direction from which the light rays come is the decisive factor in phototropic perception. He believes that if workers who have held that perception is dependent simply on differences in light intensity had considered the refraction and reflection of light in the tissue, their results, too, would have shown that light direction is determinative for phototropic response.—LOUISA E. RHINE.

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[21] BEWS, J. W., The southeast African flora: its origin, migrations, and evolutionary tendencies. Ann. Botany **36**:209–223. 1922.

[22] LUNDEGARDH, H., Zur Theorie der phototropischen Perzeption. Ber. Deutsch. Bot. Gesells. **39**:223–230. 1921.

Soil moisture and Fusarium wilt.—CLAYTON[23] has obtained some interesting results from an investigation of the relation of soil moisture to the *Fusarium* wilt of tomato. Plants in soil with low moisture content were very resistant to the disease. Any moisture shortage sufficient to check the vegetative vigor of the host checked the disease proportionally. Rapidly growing plants which had been susceptible to the disease were made disease resistant by allowing the soil to become very dry. Plants in soil with very low moisture content lost their disease resistance if rapid vegetative growth was induced by the addition of water. Plants growing in saturated soil were immune to attack, but if the moisture content was lowered the disease soon developed. The conclusion is that the immunity of plants in saturated soil is correlated with practical absence of nitrates in the host tissues.—J. M. C.

North American Flora.—The seventh and eighth parts of volume 7 continue the presentation of the Aecidiaceae by J. C. ARTHUR, in collaboration with H. S. JACKSON, E. A. MAINS, and G. R. BISBY, three genera being included. *Bullaria* includes 66 species, 52 of which are transferred from *Puccinia* in the present publication; *Teleutospora* includes 11 species, 8 of which are transferred from *Uromyces;* while *Micropuccinia* includes 149 species, 83 of which are transferred from *Puccinia*. In addition, those forms whose life cycle is not known are described under the form genera *Uromyces* (10 spp.) and *Puccinia* (43 spp).

The first part of volume 14 begins the presentation of Bryophyta, including Sphaerocarpales and Marchantiales, by M. A. HOWE, A. W. EVANS, and Miss C. C. HAYNES. Much the largest genus is *Riccia*, with 25 species, *Asterella* coming next with 15 species.—J. M. C.

Monograph of Isoetes.—Miss PFEIFFER[24] has published a very complete monograph of the Isoetaceae. The prefatory statement includes the taxonomic history, local names and economic uses, general morphology, and ecological relations. The work was done chiefly at the Herbarium of the Missouri Botanical Garden, where the collections of ENGELMANN and EATON are deposited. Numerous other collections were placed at the disposal of the author, including collections from South Africa, Australia, Tasmania, and India. In the taxonomic presentation, 64 species are recognized, 3 of which are described as new. There are also described 4 new varieties and 3 new forms. In connection with each description, the synonymy, geographical distribution, and exsiccatae examined are recorded.—J. M. C.

Apogamy in Phegopteris.—Mrs. BROWN,[25] in continuation of her studies of apogamy in ferns, has investigated *Phegopteris polypodioides*. By the use

[23] CLAYTON, E. E., The relation of soil moisture to the *Fusarium* wilt of the tomato. Amer. Jour. Bot. **10**:133–147. *pls. 13–15*. 1923.

[24] PFEIFFER, NORMA E., Monograph of the Isoetaceae. Ann. Mo. Bot. Gard. **9**:79–232. *pls. 12–19*. 1922.

[25] BROWN, MRS. E. D. W., Apogamy in *Phegopteris polypodioides*. Bull. Torr. Bot. Club **50**: 17–34. 1923.

of various solutions and cultural conditions, she has secured a wide range of responses. Among them are the following: a great range in the length of the filamentous stage of the prothallium; branching of prothallium and reversion to filamentous condition; development of both sex organs by the prothallium, and their separation on different prothallia, the sex dependent on variations in the solutions used; apogamous sporophytes in cultures on certain solutions, and also intermediate apogamous outgrowths.—J. M. C.

Polyembryony in ferns.—ETTER[26] has secured polyembryony in several ferns under experimental conditions. Dividing prothallia longitudinally, each half may be made to grow and develop two or more embryonic sporophytes, and in some cases each half may regenerate one or two heart-shaped lobes on which one or more sporophytes may be produced, as well as on the original half Parts of quartered prothallia may continue growth and develop sporophytes.—J. M. C.

Polyembryony in Vincetoxicum.—GUIGNARD[27] has given a detailed and fully illustrated account of fertilization and the occurrence of polyembryony in *Vincetoxicum*. The fertilized egg produces a mass of tissue, from which several embryos may develop, with more or less elongated suspensors. The clustered embryos, often five or six in number, develop to various stages. GUIGNARD regards this polyembryony as the normal condition in *Vincetoxicum*. —J. M. C.

Prairie and forest.—Supporting the conclusions of SHIMEK, and of POOL and WEAVER that the evaporating power of the air is one of the chief factors in the control of forests and grassland within the transition region, HANSON[28] has presented instrumental data from a small prairie area included in the deciduous forest near Peru, Nebraska. In addition to high evaporating power of the air, he found that soil moisture was very low within the grasslands, often falling below the available point.—GEO. D. FULLER.

Virginia trees.—A non-technical pocket manual of the trees of Virginia has been prepared by JONES,[29] the state forester, in co-operation with the United States Forest Service. The illustrations, the simple style in which the descriptions are given, and the pocket size of the manual should make it useful and popular within the state it is designed to serve.—GEO. D. FULLER

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[26] ETTER, AUSTIN, Polyembryony developed under experimental conditions in certain polypodiaceous ferns. Bull. Torr. Bot. Club **50**:95–106. *pl. 4. figs. 6.* 1923.

[27] GUIGNARD, L. M., La fécondation et la polyembryonie chez les *Vincetoxicum*. Mem. Acad. Sci. **57**: 1–25. *figs.* 64. 1921.

[28] HANSON, H. C., Prairie inclusions in the deciduous forest climax. Amer. Jour. Bot. **9**:330–337. *figs. 2.* 1922.

[29] JONES, CHAPIN, Common forest trees of Virginia. Univ. of Virginia Bull. *26:* pp. 64. *figs. 64.* 1922.

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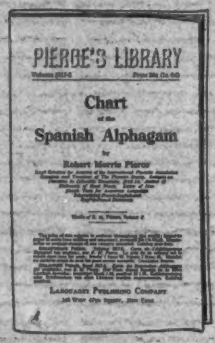

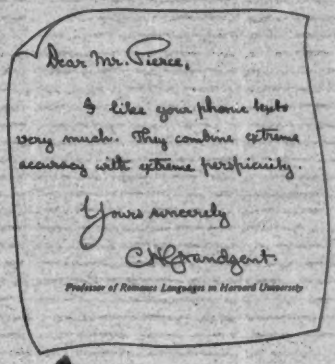
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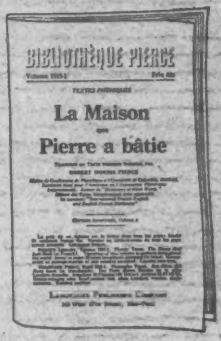

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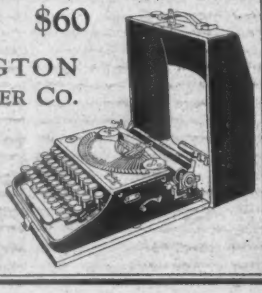

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